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Going feral: Time and propagule pressure determine range expansion of Asian house
geckos into natural environments

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Abstract

Upon establishment in a new area, invasive species may undergo a prolonged period of relatively slow population growth and spread, known as a lag period. Lag periods are, apparently, common in invasions, but studies of the factors that facilitate subsequent expansions are lacking in natural systems. We used ten semi-independent invasions of the Asian house gecko (*Hemidactylus frenatus*) to investigate which factors facilitate expansion of this human-associated species across the urban–woodland interface. We conducted 590 surveys over 12 months on ten transects running from the urban edge to 2 km into adjacent natural woodland. We recorded *H. frenatus* out to 2 km from the urban edge on nine out of ten transects, and at high abundance at many woodland sites. Body size, body condition, sex ratio and proportion of gravid females did not vary with distance from the urban edge, suggesting viable, self-sustaining populations in natural habitats. The extent of expansion was, however, strongly dependent on propagule pressure (the abundance of *H. frenatus* at the urban edge), and time (time since *H. frenatus* established in the urban area). The size of the urban area and the structure of the surrounding environment did not impact invasion. Our results show that an invasive species that is deemed ‘human-associated’ over most of its range is invading natural habitats, and propagule pressure strongly controls the lag time in this system, a finding that echoes results for establishment probability at larger scales.

Key Words: *Hemidactylus frenatus*; range expansion; urbanization; lag period; invasive species

Introduction

The impact of introduced species is often underestimated due to initial slow population growth and spread (Rilov et al. 2004; Aikio et al. 2010). This is occasionally followed by a rapid increase in range, or a population explosion, which can have devastating impacts on native biota and ecosystems (Campbell 2007). The term ‘lag period’ is used to define a period of slow population growth in an invasive species upon introduction (Sakai et al. 2001; Crooks 2005). Lags may be caused by demographic, genetic or environmental constraints, and subsequent expansions are likely facilitated by increased propagule pressure, adaptations or environmental change (Taylor and Hastings 2005; Lockwood et al. 2009; Facon et al. 2011). It is,

72 however, difficult to identify and study lags and subsequent expansions in nature
73 because the resources needed to monitor seemingly non-invasive species from
74 introduction to range expansion (which can take up to 120 years in extreme cases;
75 Rilov et al. 2004) would be excessive. It is also difficult to find replicate invasions
76 within a similar climate and region with which to compare results. As such, most field
77 studies that refer to lags use the term to explain inconsistent or unexpected findings,
78 such as unusually slow population growth upon introduction, or a sudden expansion
79 many years after establishment (Rilov et al. 2004; Sousa et al. 2009; Witte et al.
80 2010). Nonetheless, lag periods may present important windows for biological
81 control, and a better understanding of why they end could have important implications
82 for conservation (Crooks 2005).

83
84 In theory, propagule pressure will be a critically important predictor of establishment
85 success and range expansion in invasive species (Lockwood et al. 2005; Colautti et al.
86 2006; Simberloff 2009). Populations may need to reach a critical size threshold to
87 overcome Allee effects, demographic and environmental stochasticity, and genetic
88 constraints before range expansion can begin (Lockwood et al. 2005; Barton and
89 Turelli 2011). Additionally, models of niche evolution suggest that continual one-way
90 immigration from a nearby source habitat can allow populations to persist in sink
91 habitats, where they would otherwise become extinct (Gomulkiewicz et al. 1999).
92 With time, this immigration may facilitate adaptation of these populations to the sink
93 habitat, resulting in establishment and further spread (Gomulkiewicz et al. 1999; Holt
94 et al. 2003). Thus, increased propagule pressure, by sustaining a marginal population
95 and increasing its genetic diversity, may facilitate the evolution of that marginal
96 population so that it is no longer a sink, but a source for further invasion (Polechová
97 et al. 2009).

98
99 Human-associated species offer ideal systems to investigate the factors that facilitate
100 expansion of invasive species after lag periods. These species thrive in urban areas,
101 and have often been associated with humans for so long that their natural habitat in
102 the native range is poorly known (Keller 2007). Examples of human-associated
103 species include house sparrows (*Passer domesticus*), pigeons (*Columba livia*),
104 common mynas (*Acridotheres tristis*), house mice (*Mus musculus*), house geckos
105 (e.g., *Hemidactylus frenatus*), and American cockroaches (*Periplaneta americana*)
106 (Dame and Petren 2006; Manor et al. 2008; Shochat et al. 2010; Sætre et al. 2012;
107 Martin et al. 2015). Such animals are rarely introduced intentionally, but continue to

spread rapidly as passengers in human development (Jeschke and Strayer 2006; Wilson et al. 2009; Chapple et al. 2012). They establish readily in new regions, because urban areas are fairly similar environments wherever they occur; however, they are seldom considered a threat to natural habitats because of their perceived restriction to human modified areas. Despite this, some 'human-associated species' do spread into natural environments, and these can provide important insights into the factors that facilitate range expansion in invasive species (Holway 1998; Kanda et al. 2009).

The strong differences between urban and natural environments, and the variation in these differences across large introduced ranges, make human-associated species valuable systems for understanding the dynamics of range edges. Variation in the urban/natural transition is determined by the physical and biological nature of the adjacent habitat types and also by human degradation of adjacent natural habitats. Degradation may enable human-associated species to move away from urban settlements by increasing the suitability of the surrounding environment (Didham et al. 2005; Bolger 2007). Hence, degraded adjacent habitats may provide a gentler cline in habitat variation, to which populations may more easily adapt (Kirkpatrick and Barton 1997). Urban populations of human associated species differ in population age, size, density and connectivity, and the surrounding natural habitat is degraded to varying extents. This variation, over multiple invasion fronts, allows empirical assessment of the factors that facilitate range expansion into surrounding habitat.

While human-associated invasive species offer a powerful system to investigate range expansion, they are, for a number of reasons, also a growing conservation concern. First, urbanisation and fragmentation are increasing, bringing more human settlements, infrastructure and transport networks in contact with natural environments (Marvier et al. 2004; Rand et al. 2006; Stewart et al. 2006; McDonald et al. 2008). A declining proportion of the world's natural habitats fall in truly wild areas. Second, human-associated species often have large non-native distributions, bringing them into contact with a myriad of different natural habitats across different regions of their introduced range (Carranza and Arnold 2006; Tollenaere et al. 2010). It is possible that at least some of these habitats will be suitable for invasion, and it is likely that a species restricted to urban environments in one region, could invade adjacent natural areas in another. Finally, the favourable conditions in anthropogenic environments may facilitate growth of large populations, which could act as sources

for expansion into adjacent natural habitats (Kanda et al. 2009; Møller et al. 2015). For these reasons it is vital to understand what drives range expansion in human-associated species.

The Asian House Gecko

The Asian house gecko, *Hemidactylus frenatus*, is native to Southeast Asia, although its long history as a human-associated species means that its original native distribution is not clear (Carranza and Arnold 2006; Hoskin 2011). It is one of the world's most widespread terrestrial reptiles, and its range continues to expand globally through the tropics and subtropics (Hoskin 2011). The current distribution of *H. frenatus* includes parts of South-East Asia, Japan, southern USA, Mexico, parts of Central and South America, Madagascar, Kenya, Australia, and islands in the Atlantic, Indian and Pacific Oceans (Lever 2006; Rodder et al. 2008; Hoskin 2011). The species spreads readily with international cargo transport, along transport networks within regions, and through urban areas (Hoskin 2011): a multimodal pattern of dispersal reported for other invasive gecko species globally (e.g., Short and Petren 2012).

Hemidactylus frenatus is abundant in urban areas and on isolated buildings, but is rarely recorded in natural habitats, even in its native range (Hoskin 2011). The biology of *H. frenatus* is generally believed to be tied to human structures—it forages on buildings, particularly around lights, and anthropogenic structures provide refuge sites and thermal buffering in colder parts of the invasive range (Carranza and Arnold 2006; Amey 2013; Lei and Booth 2014). Therefore, this species is considered to be human-associated, being largely restricted to urban areas. There have been localised reports of *H. frenatus* occurring in natural environments across its introduced range (Hoskin 2011), but these are typically considered to be vagrants from nearby built areas. An exception is the Mascarene Islands, where *H. frenatus* was found to be abundant through most natural habitats and to have out-competed native *Nactus* gecko species (Cole et al. 2005). Most records from natural habitats are from oceanic islands with relatively depauperate reptile communities, and it has been argued that *H. frenatus* may only be able to colonise natural environments in these settings (Vanderduys & Kutt 2013). Therefore, to date *H. frenatus* has been treated as a highly invasive gecko that has few conservation implications because it rarely strays beyond the urban edge (Kluge 1969; Low 1999; Wilson and Swan 2008; Vanderduys and Kutt 2013).

Hemidactylus frenatus was accidentally introduced into Australia with shipping cargo in the 1960s (Hoskin 2011). Australia is a global centre of gecko diversity and endemism, with 158 species in 24 genera and three families (Macdonald 2015). Gecko abundance is also disproportionately high in Australia and geckos are a conspicuous component of Australian biodiversity, especially in the tropical and subtropical parts of the country. Since its introduction, *H. frenatus* has spread rapidly through urban areas of northern and eastern Australia (Figure 1; Hoskin 2011). Given Australia's suitability for geckos, Hoskin (2011) argued that we should be concerned about the potential for *H. frenatus* to establish in Australia's natural habitats. In this study we use *H. frenatus* as a model system to investigate the factors that facilitate range expansion of human-associated species after a lag period. We quantify invasion into natural habitats around the city of Townsville in north-east Australia, where *H. frenatus* has been present since about 1980. We test a number of potential determinants of invasion across the urban–woodland interface, including propagule pressure, establishment time, and the structure of the urban and natural habitats.

Methods

Field Sampling

This study was conducted in the Townsville region of north Queensland. Townsville is a city of approximately 200,000 people and the main habitat type abutting urban areas is dry sclerophyll woodland (herein termed 'woodland'). This habitat consists of scattered large *Eucalyptus* trees and an understory of grasses and scattered saplings and bushes (Supp. Fig. 4). Ten transects, each running from an urban edge into adjacent woodland, were established in May 2013 (Fig. 1). Google Earth™ was used to choose the location of these transects, with the objective being to sample independent or semi-independent transects across the Townsville region where urban areas abutted natural woodland (Fig. 1). Each transect was approximately linear and contained five survey sites, each positioned 500m apart. Site 1 was amongst houses on the urban edge, and the subsequent four sites extended to 2km into the woodland (Fig. 1). The ten transect names and their abbreviations are: Toomulla (TO), Toolakea (TK), Bluewater Park (BP), Yabulu (YA), the Australian Institute for Marine Science (AI), Cungulla (CU), Mount Elliot (ME), Town Common (TC), Mount Stuart (MS) and Magnetic Island (MI).

Nine of these transects were surveyed for geckos 12 times (approximately once a month) between May 2013 to April 2014. The tenth transect at Yabulu (YA) was first visited in July 2013 and was surveyed ten times. This gave a total of 590 gecko surveys over the year. The five sites on each transect were surveyed on the same night, and site order was randomised. Each survey was a 15-minute search, which involved slowly walking in a straight line from the site marker and locating geckos by their eye-shine. All geckos seen were recorded and the age class of each individual (i.e. juvenile, sub-adult or adult) was estimated visually. We also attempted to catch and measure five *H. frenatus* during each survey (this commenced during the fourth month of sampling). Captured geckos were placed inside a small snap-lock bag and weighed using a 10 g Pesola™ spring balance. Snout–vent length (SVL) was measured using a small plastic ruler. Sex was determined by looking for the enlarged testis bulges of males. Females were examined for eggs visible through the ventral skin (as in McKay and Phillips 2012) and reproductive state was recorded. Each gecko was then released at the point of capture. The timer was paused while measuring and weighing geckos. Each gecko survey was conducted by two people, Louise Barnett and one other (who varied across surveys but was trained in spotlighting and gecko identification).

Environmental variables

In order to resolve the determinants of range expansion, we measured the following variables across transects: 1. the characteristics of human settlement in the area (housing density of the urban area, distance from each site to the urban edge, distance from each site to the nearest structure); 2. the estimated date of *H. frenatus* arrival in the urban area; and, 3. the structure of adjacent natural habitat (tree density at each site).

Housing density in the urban area was calculated by counting all structures within 1 km of the urban edge on Google Earth Pro™. This program was also used to measure the distance from each site to the nearest structure, and the distance from each site to the urban edge. *Hemidactylus frenatus* excel at human mediated jump dispersal (Hoskin 2011), and are observed to rapidly invade new housing developments in Townsville (authors, pers. obs). Therefore, colonisation time of each urban area was based on an estimate of when housing development occurred in that area. This was estimated using a real estate website (onthehouse.com.au) to find the earliest house sale in each urban area (as an estimate of urban development in each area), and a

selection of these dates were ‘ground-truthed’ by querying residents in that urban area as to the age of their houses. Dates prior to 1980 were set to 1980 because that is the estimated year of arrival of *H. frenatus* in Townsville (Queensland Museum records; Hoskin 2011). The coarse structure of adjacent habitat was measured as tree density at each site, via the Bitterlich sweep method (Bitterlich 1984). Tree density was used as an estimate of the suitability of adjacent habitat (more trees = better habitat for an arboreal gecko) and as an estimate of habitat degradation (visually higher quality woodland generally had a higher Bitterlich value).

Statistical analyses

All analyses were conducted in R version 3.1.1 (R Core Team, 2014). We used linear mixed effects models (LMMs) or generalised linear mixed effects models (GLMMs) within the ‘lme4’ package for all analyses (Bates *et al.* 2014). All variables were mean-centred and standardised before analysis.

Does *H. frenatus* occur in natural habitats?

Basic counts and plots were used to assess *H. frenatus* presence/absence and abundance at the woodland sites. More detailed analyses of the determinants of abundance at sites are covered in a section below.

Are *H. frenatus* populations in natural habitats self-sustaining?

To determine whether the populations at woodland sites are self-sustaining, we analysed five variables that we deemed indicators of *H. frenatus* population ‘health’: 1. Snout-vent length (SVL), 2. Body condition index (BCI), 3. Population sex ratio, 4. Proportion of females that were gravid, and 5. Proportion of juveniles.

We used distance from the urban edge as an independent variable in all analyses to investigate whether populations differed depending on distance from the source habitat. It is, however, difficult to distinguish between the effects of distance and habitat (urban vs. woodland), because these two variables were highly correlated ($r^2 = 0.77$; the urban site was always Site 1). Therefore, we also fitted models using habitat as a categorical factor (urban vs. woodland). We compared the Akaike Information Criteria of the distance and habitat models to assess the best fitting predictor for each question (supplementary table).

‘Transect’ was used as a random effect in all analyses to account for any non-independence at that level. Seasonal effects were also included in models to correct for seasonal variation in abundance. These were fitted by converting the day of year of each survey into degrees ($day\ of\ year \times \frac{360}{365}$), then radians ($day\ in\ degrees \times \frac{\pi}{180}$) and expressing this as the sine and cosine. Converting the day of year into two circular variables (sine and cosine) allowed us to fit sinusoidal curves to the models (Crawley 2007). A significant p-value in either cosine(day of year) or sine(day of year) indicates that seasonal variation is important.

BCI was derived from the residuals of a linear regression between log-transformed SVL and log-transformed mass (Townsend et al. 2007). BCI was only calculated for those geckos with an original tail. LMMs were used to assess whether distance from the urban edge or seasonal variation affected SVL and BCI. The Satterthwaite approximation was used to generate p-values for these models through the ‘lmerTest’ package (Kuznetsova et al. 2015). Where the response variable was proportional (e.g., the proportion of gravid females), GLMMs with a binomial error structure were used.

Factors that facilitate invasion of the woodland

To establish which factors facilitated colonisation of natural environments, we used a GLMM with a negative binomial error structure to correct for over dispersion. The dependent variable in this analysis was total number of *H. frenatus* found at each of the ‘woodland’ sites (i.e. 0.5–2 km from the urban edge). The independent variables were propagule pressure (the mean number of *H. frenatus* found at the urban edge site), the number of structures within 1 km of the urban edge, colonisation time (the amount of time *H. frenatus* had been present in the urban area), the structural complexity of habitats, the distance from each site to the nearest structure, and distance from each site to the urban edge. We also included the interaction between distance from each site to the urban edge and colonisation time to assess whether the populations with more time available to them were more likely to be found farther from the urban edge.

Results

Does *H. frenatus* occur in natural habitats?

Hemidactylus frenatus were recorded at least once at every woodland site at nine out of the ten transects (Fig. 2). They were therefore recorded at 36 of the 40 woodland sites. The only sites where *H. frenatus* was not recorded were the four woodland sites on the ME transect (Fig. 2). Patterns of invasion into woodland on the transects ranged from high abundance out to the furthest site at 2 km (TC, MI, AI, TO), general decline of *H. frenatus* further into the woodland (CC, MS), evenly low abundance at woodland sites (TK, YA, BP), to absent at all woodland sites (ME) (Fig. 2). Analysis of the determinants of woodland invasion across the transects is presented in a section below.

Detailed comparisons of the abundance of *H. frenatus* and native geckos on the transects will be dealt with in a future publication; however, we provide some summary statistics here to assess the abundance of *H. frenatus* at woodland sites compared to native geckos in this region. The average number of *H. frenatus* found per survey at woodland sites (3.14 individuals) was considerably higher than the average number of native geckos (all species combined) per survey at woodland sites (0.87 individuals), even when compared against native gecko abundance at sites where *H. frenatus* was not recorded (1.68 individuals/survey).

Are *H. frenatus* populations in natural habitats self-sustaining?

There was no difference in model fit (based on AIC) between the distance and habitat models, for gecko size or gecko body condition, sex ratio, or proportion of gravid females (Supp. Table 1), so we present the results of the distance models (Fig. 3; Fig. 4A) because those best fit the original rationale of using transects with sites at increasing distance from the urban edge. In contrast, the habitat model appeared to be a better fit for proportion of juveniles ($\Delta\text{AIC} = 5.09$, Supp. Table 1) and therefore this result was presented based on the habitat model (Fig. 4B).

There was a significant seasonal difference in gecko size (SVL) ($\cos(\text{day})$: $z = 6.03$, $p = 0.001$; $\sin(\text{day})$: $z = 2.58$, $p < 0.01$) (Supp. Fig. 1A) and condition (BCI) ($\cos(\text{day})$: $z = -3.16$, $p < 0.01$; $\sin(\text{day})$: $z = 0.24$, $p = 0.81$) (Supp. Fig. 1B) (Supp. Table 2), with smaller geckos, in poorer condition being found towards the middle of the year (Supp. Fig. 1). However, neither SVL ($z = 1.03$, $p = 0.30$) (Fig. 3A) nor body condition ($z = 1.24$, $p = 0.22$) (Fig. 3B) varied significantly with distance from the urban edge (Supp. Table 2).

Sex ratio was not related to distance from the urban edge ($z = 1.35$, $p = 0.18$, Supp. Fig. 2A) and did not vary through the year ($\cosine(\text{day})$: $z = -0.12$, $p = 0.91$; $\sin(\text{day})$: $z = -0.53$, $p = 0.59$, Supp. Fig. 2B) (Supp. Table 2). There was significant seasonal variation in the proportion of females that were gravid at sites ($\cosine(\text{day})$: $z = 2.71$, $p < 0.01$; $\sin(\text{day})$: $z = 2.36$, $p = 0.02$), with more females gravid in summer (Supp. Fig. 3A). The proportion of gravid females was not, however, significantly related to distance from the urban edge ($z = 1.42$, $p = 0.16$, Fig. 4A). There was significant seasonal variation in the proportion of juveniles at sites ($\cosine(\text{day})$: $z = -5.34$, $p < 0.001$; $\sin(\text{day})$: $z = 1.35$, $p = 0.18$), with more juveniles seen during winter (Supp. Fig. 3B) (Supp. Table 1). The proportion of juvenile *H. frenatus* at sites decreased significantly with distance from the urban edge ($z = -3.79$, $p < 0.001$; Supp. Table 1); however, as mentioned above, the habitat model was a better fit for this data, with a significantly higher proportion of juveniles at the urban edge than in the adjacent woodland sites ($z = 4.5$, $p < 0.001$; Supp. Table 2; Fig. 4B).

Factors that facilitate invasion of the woodland

Hemidactylus frenatus were recorded at most woodland sites, but abundance of *H. frenatus* at these sites varied among transects (Fig. 2). Analysis of the determinants of invasion revealed that higher propagule pressure (i.e., the mean number of geckos at the urban edge site) was significantly associated with higher counts in the woodland ($z = 6.10$, $p < 0.001$, Table 1.). Distance from the urban edge did not directly affect the abundance of *H. frenatus* in the woodland ($z = -0.123$, $p = 0.38$), but there was, however, a significant positive interaction between colonisation time and distance from the urban edge ($z = 2.71$, $p < 0.01$, Table 1). Time as a factor on its own was borderline significant ($z = 1.95$, $p = 0.051$). Neither the distance to the nearest structure ($z = -0.44$, $p = 0.66$), the number of structures within 1 km of the urban edge ($z = 0.98$, $p = 0.32$), nor natural habitat structure (tree density) ($z = 1.66$, $p = 0.09$) significantly affected the number of geckos in the woodland (Table 1.).

Discussion

Can 'human-associated' species establish in natural habitats?

Our study was designed to investigate the factors that facilitate the invasion of a supposedly human-associated species into natural habitats. Before we can usefully address these factors, however, we need to establish that we have a system in which successful invasion is happening. Our data show that a gecko generally considered tied to urban areas across its range, has established in natural woodland in the Townsville region. Our results present multiple lines of evidence demonstrating that *H. frenatus* in natural habitats represent established populations and are not merely individuals dispersing out from the urban edge. First, we recorded *H. frenatus* at 36 out of 40 woodland sites, including out to 2 km from the urban edge at nine of the ten transects. This is further than could be explained by movement of individual geckos, which typically have movement and dispersal abilities one to two orders of magnitude lower than this (Hoehn et al. 2007; Dubey et al. 2012; Paulissen et al. 2013). Second, although *H. frenatus* are more common on the urban edge, they were still found in substantial numbers at many woodland sites (Fig. 2). These abundances were over three times higher than those of native geckos (all species combined) at the same woodland sites

The third line of evidence indicating that these are established populations is that individuals in woodland habitats were in good condition—we found no difference in size or body condition up to 2 km from the urban edge. Finally, the geckos are clearly breeding in natural habitats: there were no differences in sex ratio or proportion of gravid females from the urban edge out to 2 km. Additionally, although proportion of juveniles was lower at woodland sites (discussed below), juveniles were observed in most woodland sites, indicating that recruitment is occurring. Our results unequivocally demonstrate established, breeding populations of *H. frenatus* in woodland environments in the Townsville region.

Although *H. frenatus* are present and reproducing in many woodland habitats, abundance is higher at urban sites compared to woodland sites (Fig. 2A). Urban areas appear to have a higher carrying capacity than natural habitats. This could be due to several factors: high abundances of insects around lights; more variable surface types for arboreal geckos (buildings, fences, rockeries, garden plants); and buildings that provide refuge sites and thermal buffering. So although *H. frenatus* can establish in natural environments, abundance may always be higher in urban areas. Nonetheless, the lower abundance of *H. frenatus* in woodland habitats should not be taken as a lack

of establishment success or potential impact. It is worth reiterating that *H. frenatus* were over three times more abundant than native geckos in woodland sites.

Although we found breeding populations of *H. frenatus* in natural habitats, these woodland populations had a significantly lower proportion of juveniles. Comparison of the distance model (smooth cline) and the habitat model (stepped cline) suggested that the proportion of juveniles was best described as a stepped transition from urban to woodland habitat rather than a gradual decline with distance (Supp. Table 1, Fig. 4B). The simplest explanation for this pattern is lower detectability of small, cryptic juveniles in woodland. Alternatively, given the proportion of gravid females was constant with regard to distance/habitat, our results here may indicate that juvenile survivorship is lower in the woodland compared with urban habitats. The structural complexity of urban habitats (with walls, fences, shrubs and trees), for example, could facilitate survival of eggs and juveniles through providing both thermal buffering and predator retreat sites (Lei and Booth 2014). Furthermore, cannibalism has been reported in *H. frenatus* (Bolger and Case 1992), and may be a primary source of mortality for juveniles. For this to be the driver of reduced juvenile survival in the woodland would require greater contact rates between adults and juveniles in woodland habitats. Given that these woodland habitats appear to support a lower density of geckos overall (and so should have lower rates of interaction between individuals), higher rates of cannibalism in woodland areas seem unlikely. Overall then, we suspect the observed step shift in juvenile abundance between urban and woodland sites reflects a step shift in detection probability, rather than a change in juvenile survivorship.

What factors determine the rate of invasion of natural habitats?

While we found *H. frenatus* in many natural habitats, there was large variation in the degree of expansion in woodland environments on the ten transects around Townsville. We assessed several factors considered to be potential determinants of range expansion in invasive species: propagule pressure (density of geckos at the urban edge), establishment time of geckos at the nearest urban area, distance to the nearest structure, the number of structures within 1 km of the urban edge, and the structure of the natural habitats. Of these, the abundance of *H. frenatus* in woodland habitats was most strongly related to: (i) propagule pressure (abundance of geckos at the urban edge), and (ii) the interaction between colonisation time and distance from

the urban edge. The effect of time on distance in our analysis indicates that the longer *H. frenatus* has been established in the urban area, the more extensive their spread into the woodland.

Propagule pressure has repeatedly been shown, at the macroecological level, to be an important determinant of establishment success (Holle and Simberloff 2005; Lockwood et al. 2005; Colautti et al. 2006). Whether or not a species establishes a population in a new locality is strongly contingent on propagule pressure. Our results show that propagule pressure is also important to continuous range expansion across differential habitats. In this context, propagule pressure does more than just increase the chances that an invasive species will establish at a new site. In continuous populations, increased propagule pressure may assist marginal populations overcome the Allee effects that can halt range advance (Barton and Turelli 2011). As well as this it may provide genetic diversity necessary for these marginal populations to adapt to conditions in the new habitat (Polechová et al. 2009).

The other potential determinants of invasion we tested were not significant. These included distance to the nearest structure, urban housing density (number of structures within 1 km of the urban edge), and the structural complexity of natural habitats. The natural environments in this study were variable, from degraded woodland through to high quality woodland. Our measure of tree density coarsely captured this variation, with visually more degraded woodlands having generally lower tree density values. We found that *H. frenatus* were just as likely to invade adjacent woodland regardless of habitat structure. This is interesting because others have suggested that *H. frenatus* and other human-associated species will only invade degraded habitats (Didham et al. 2005; Vanderduys and Kutt 2013). The urban areas in our study were also variable, ranging from transects on the edge of large urban areas with high-density housing to transects on the edge of small, low density, semi-rural areas (Fig. 1). The fact that urban housing density has no effect on colonisation success indicates that even small settlements, or perhaps even a single remote building, could potentially act as source populations for *H. frenatus* to establish in woodland.

Hemidactylus frenatus has established in tropical areas around the world, yet there have been only a handful of records from natural environments, and most of these reports are from island systems where competition from other gecko species is low (reviewed in Hoskin 2011). The demonstrated successful establishment of *H. frenatus*

in natural environments in the Townsville region, where there are numerous native gecko species in woodland sites, is therefore of some significance. Our study places the numerous anecdotal observations of *H. frenatus* in natural habitats of northern Australia (Hoskin 2011) onto a quantitative footing; not all of these observations reflect vagrant individuals. How general this pattern of slow invasion across the urban-natural transition is, remains to be established. It is possible that Australia is particularly suitable for geckos (supported by the high diversity and abundance of native geckos) and so this is a pattern that will only occur in the Australian range of *H. frenatus*. Another possibility is that invasion of natural habitats is also happening elsewhere, but is not being detected or is being incorrectly attributed to ‘spillover’ from urban areas into natural areas (i.e., immigration, but no population growth in natural areas).

Our analyses also show that time is important for successful expansion into natural habitats. Given that *H. frenatus* is a relatively recent arrival in many regions, populations may not yet have had time to establish in natural habitats. Our results suggest that, given time, and sufficient propagule pressure, *Hemidactylus frenatus* may well commence to invade natural habitats in other parts of its rapidly expanding global range, achieving biologically important densities in non-urban areas. Nonetheless, the gecko is a small reptile with low dispersal capabilities, so diffusive spread will always be a slow process. Furthermore, in some areas urban development is occurring rapidly, potentially faster than *H. frenatus* is establishing and spreading in adjacent natural environments. In these areas, woodland populations may be replaced by urban development faster than the gecko populations are establishing and spreading.

Broader conclusions

Introduced species that spread into natural ecosystems can have serious impacts on biodiversity, but invasion is often overlooked due to long lag periods of low density. Through fine-scale assessment of multiple populations at different stages of invasion we disentangled the factors that facilitate expansion of a ‘human-associated species’ into natural habitats. We found that time and propagule pressure are the primary determinants of invasion of Asian house geckos into novel habitats. While our study investigates range dynamics of a single species, our findings are in broad agreement with patterns seen at the macro-ecological level: propagule pressure and time are

important drivers of establishment success for invasive species generally (Colautti et al. 2006; Lockwood et al. 2009; Simberloff 2009). Here we show that these factors are also important at the local level – influencing the rate at which populations invade into novel habitats.

Most generally, our finding that a species typically considered a human commensal is successfully invading nearby non-urban areas reinforces the concept that lags in range expansion should be anticipated for many invasive species, especially those spreading into a novel habitat. Most studies of invasive species are conducted when a known ‘problem’ species is first introduced, or when an invasive species becomes an obvious problem. It is important to monitor potentially latent invasive species on the range edge—the interface between urban and natural habitats. Understanding the factors that facilitate expansion may allow us to prevent these latent invasive species from realising their potential.

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Figures and tables

Figure 1. The study area with the location of each transect (black line with a two-letter code) in relation to urban areas (dark grey). Transect codes are defined in the Methods. The layout of sites on each transect is shown in the inset bottom left. The inset map shows the broad distribution of *H. frenatus* in Australia (from Hoskin 2011), with the red box showing the study area.

Figure 2. (a) The total number of *H. frenatus* found during the 12 months of surveys at each transect with distance from the urban edge. Estimated dates of *H. frenatus* arrival in urban areas are listed on the right. **(b)** The number of *H. frenatus* found per survey with distance from the urban edge. Outliers are indicated by black dots above the boxplots.

Figure 3. (a) Snout-vent length (SVL) of captured *H. frenatus* with distance from the urban edge and, **(b)** body condition index of captured *H. frenatus* with distance from the urban edge.

Figure 4. (a) The proportion of gravid female *H. frenatus* found on each survey with distance from the urban edge. The line and confidence intervals are derived from the distance model. **(b)** The proportion of juvenile *H. frenatus* captured in each survey against distance from the urban edge. The line and confidence intervals are derived from the habitat (urban/woodland) model and highlight the stepped cline in the proportion of juveniles from urban areas (0 m) into the woodland (500 m to 2 km). See Results for details on why (a) is presented as a distance model and (b) is presented as a habitat model.

Table 1. Factors that determine invasion success of *H. frenatus* in woodland environments as determined by a negative binomial generalised linear mixed effects model.

Parameter	Model output			
	Estimate	Standard error	T-value	P-value
Intercept	0.50	0.16	3.12	0.002
Nearest structure (km)	-0.07	0.15	-0.44	0.664
No. structures	0.10	0.10	0.99	0.324
Habitat structure	0.17	0.11	1.66	0.097
Propagule pressure ***	0.95	0.16	6.10	< 0.0001
Time *	0.31	0.16	1.95	0.051
Distance from urban edge	-0.12	0.14	-0.88	0.380
Distance x Time **	0.24	0.10	2.71	0.007

* $P \leq 0.05$

** $P < 0.01$

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