The pitfalls of short-range endemism: high vulnerability to ecological and landscape traps

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Ecological traps attract biota to low-quality habitats. Landscape traps are zones caught in a vortex of spiraling degradation. Here, we demonstrate how short-range endemic traits may make such taxa vulnerable to ecological and landscape traps. Three short-range endemic species of mygalomorph spider were used in this study: *Idiommata blackwalli, Idiosoma sigillatum* and an undescribed *Aganippe sp*. Mygalomorphs can be long-lived (> 40 years) and select sites for permanent burrows in their early dispersal phase. Spiderlings from two species, *I. blackwalli* (n=20) and *Aganippe sp.* (n=50), demonstrated choice for microhabitats under experimental conditions, that correspond to where adults typically occur *in situ*. An invasive veldt grass microhabitat was selected almost exclusively by spiderlings of *I. sigillatum*. At present, habitat dominated by veldt grass in Perth, Western Australia, has lower prey diversity and abundance than undisturbed habitats and therefore may act as an ecological trap for this species. Furthermore, as a homogenising force, veldt grass can spread to form a landscape trap in naturally heterogeneous ecosystems. Selection of specialised microhabitats of short-range endemics may explain high extinction rates in old, stable landscapes undergoing (human-induced) rapid change.

The pitfalls of short-range endemism: high vulnerability to ecological and landscape traps

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Abstract

Ecological traps attract biota to low-quality habitats. Landscape traps are zones caught in a vortex of spiraling degradation. Here, we demonstrate how short-range endemic traits may make such taxa vulnerable to ecological and landscape traps.

Three short-range endemic species of mygalomorph spider were used in this study: *Idiommata blackwalli, Idiosoma sigillatum* and an undescribed *Aganippe sp*. Mygalomorphs can be long-lived (> 40 years) and select sites for permanent burrows in their early dispersal phase.

Spiderlings from two species, *I. blackwalli* (n=20) and *Aganippe sp.* (n=50), demonstrated choice for microhabitats under experimental conditions, that correspond to where adults typically occur *in situ*. An invasive veldt grass microhabitat was selected almost exclusively by spiderlings of *I. sigillatum*.

At present, habitat dominated by veldt grass in Perth, Western Australia, has lower prey diversity and abundance than undisturbed habitats and therefore may act as an ecological trap for this species. Furthermore, as a homogenising force, veldt grass can spread to form a landscape trap in naturally heterogeneous ecosystems.

Selection of specialised microhabitats of short-range endemics may explain high extinction rates in old, stable landscapes undergoing (human-induced) rapid change.

Introduction

Habitat-selection theory suggests behavioural and life history decisions prompted by environmental cues act as indicators of habitats that maximise fitness (Rosenzweig, 1981). Misguided habitat choice may be based on environmental cues associated with

high-quality habitats but that are no longer reliable in disturbed or changing environments. Choices based on such cues lead to organisms entering 'ecological traps' (Delibes, Gaona & Ferreras, 2001; Dwernychuk & Boag, 1972). Ecological traps pose a serious conservation concern for a wide range of taxa (Battin, 2004; Hale & Swearer, 2016; Hale, Treml & Swearer, 2015). A review of ecological traps shows that historically, most studies have focused on highly mobile bird species and their choice of nesting sites but more recently there has been attention to other, commercially relevant, taxa (Robertson, Rehage & Sih, 2013). Here we argue that ecological traps are particularly threatening for short-range endemic (SRE) taxa. Persistence of these taxa is further compromised in disturbed landscapes for two main reasons 1) their specialist co-evolutionary requirements, and 2) limitations in their capacity to relocate following disturbance.

Highly disturbed landscapes form 'landscape traps', compromising ecological function and compounding the influence of ecological traps for many taxa (Lindenmayer et al., 2011). For example, logging and altered fire regimes can interact in ways that cause the irreversible modification of ecological function. Landscape traps may also be associated with negative feedback loops between fire and weed invasion (Fisher, Loneragan, Dixon, Delaney, et al., 2009). Thus, fire provides opportunity for weed invasion, which then provides greater fuel loads, increasing the capacity for more intense fires.

Regions with high proportions of endemic taxa represent a unique and ongoing challenge in conservation biology worldwide (Wardell-Johnson & Horwitz, 1996).

Landscape age may explain high endemism and biodiversity in some sites (Mucina & Wardell-Johnson, 2011) with complex microhabitats and niche partitioning having established and evolved over time in stable conditions (Rosenzweig, 1981). Old, stable landscapes may therefore be more susceptible to landscape traps due to increased numbers of associations – providing a higher chance of disturbances that lead to negative feedback loops (Lindenmayer *et al.*, 2011). Historical divergence in old, stable landscapes may be primarily attributed to two major factors 1) heterogeneously distributed habitat and narrow, subdued geographical barriers (Wardell-Johnson & Horwitz, 1996), and 2) taxa with limited mobility and dispersal capabilities (Rix et al., 2014).

A taxon with a distribution of less than 10 000 km^2; low reproductive output and limited mobility and dispersal are criteria for SRE taxa (Harvey, 2002). SREs are of high conservation concern as a restricted distribution contributes to rarity and increased chance of extinction (Harvey, 2002; Rabinowitz, 1981). Vulnerability is exacerbated when combined with a limited capacity to adapt or escape human-induced rapid environmental change (HIREC) (Sih, Ferrari & Harris, 2011). SREs tend to be specialists, and representation is proportionally higher in invertebrates than vertebrates (Harvey, 2002). Old, stable landscapes are likely to have the highest numbers and proportions of SREs globally (Rix *et al.*, 2014).

The ancient and highly heterogeneous landscape of south-western Australia (SWA) hosts many SRE species (Rix et al., 2016). By their nature, SREs are typically rare and

78 cryptic, making it difficult to gather essential information for conservation decisions.
79 Poor dispersal capabilities suggest that SREs are able to survive in small patches of
80 high-quality remnant vegetation (Mason, Wardell-Johnson & Main, 2016). Mygalomorph
81 spiders are excellent candidate taxa as bioindicators for SRE taxa. They are sedentary,
82 meaning individuals can be monitored long-term. Choice of microhabitat by a dispersing
83 spiderling is a vital first step to successful investment in a life-long burrow. Burrows are
84 investments in terms of effort and time to establish. It is rare for mygalomorphs to move
85 as adults, as such moves come at high energy cost and leave them vulnerable to
86 predation and desiccation (Mason et al., 2013). As mygalomorph matriarchs can live up
87 to 40 years (Main unpublished data; cited in Rix *et al.* 2016), appropriate burrow-site
88 and habitat choice by spiderlings is vital.
89
90 We aimed to determine whether mygalomorph spiderlings of three species display
91 choice of microhabitat conditions that reflects their realised niche as adults. Realised
92 niche was recorded as adult burrow microhabitats that were regularly recorded during
93 an extensive survey. Burrow microhabitats of adults of each species were used to
94 inform the microhabitat habitat preference choices provided to all spiderling species.
95 Mason *et al.,* (2016) suggested that invasive veldt grass (*Erharta* spp.) may be
96 detrimental to local mygalomorph species, either through preventing establishment of
97 burrows, or through microhabitat or prey availability variables. Veldt grass was therefore
98 made available as one of four ground cover choices for mygalomorph spiderlings in a
99 controlled field trial. Microhabitat variables of relative humidity (RH), ambient

100 temperature (Ta) and prey species assemblages (PSA) were also measured to explain
101 spiderling choice.
102
103 **Methods**
104
105 **Study site**
106 This study was conducted in Perth, a highly urbanised centre in the Mediterranean-
107 climate zone (mean annual rainfall 740 mm) of SWA. This highly biodiverse region has
108 lost almost 90% of the original habitat due to extensive deforestation and on-going
109 disturbance, qualifying it as a global biodiversity hotspot (Myers et al., 2000;
110 Wardell-Johnson et al., 2016).
111
112 **Study species**
113 We collected an individual *Idiommata blackwalli* (Barychelidae - brush-footed trapdoor
114 spiders, body length: 32 mm) with a brood size of 42 and individuals of two genera of
115 Idiopodae (armoured trapdoor spiders); an *Aganippe* sp. (body length: 27 mm) and an
116 *Idiosoma sigillatum* (body length: 36 mm) which had broods of 65 and 78, respectively.
117 The idiopid spiderlings were approximately 3 mm in length and those of *I. blackwalli* 7
118 mm long.
119 Despite large superficial differences between *Aganippe* and *Idiosoma,* genetic
120 techniques have recently found these genera to be closely related. The extreme
121 sclerotisation of the abdomens of *I. sigillatum* likely relates to behaviour where they
122 block their burrow against intruders. Burrow morphology supports this behaviour by

123 having a diagonistic ‘atrium’ where the spider can manoeuvre near their lid burrow
124 during foraging, but tightly constricts down the shaft. Foraging range is thought to be
125 enhanced for *I.sigillatum* due to their burrows having twig-line attachments; this enables
126 them to detect prey species along the twigs via vibrations. Both *Aganippe* and *Idiosoma*
127 are highly defensive of their burrows, retreating to the bottom and rearing when
128 disturbed. Conversely, the *I.blackwalli* collected was quite docile by comparison and
129 easily observable in her shallow (15 cm deep) bulb-shaped burrow. Photos of each
130 spider species and their typical burrow entrance has been provided for comparison
131 (Figure 1).
132
133 **Microhabitat preference**
134 Adult spider burrows were located during an extensive survey of Perth urban remnant
135 vegetation that included 135 quadrats (100 m x 100 m) in 41 sites (see Mason *et al.*
136 2016 for further details). Microhabitat variables to included leaf litter cover (%) and leaf
137 litter type within a one metre square quadrat centred on burrows.
138
139 To reflect the natural dispersal time of mygalomorph species a habitat preference
140 experiment was conducted, using the collected spiderlings, from 24th April to 24th May in
141 the field trials area at Curtin University (Bentley campus). Fifty circular enclosures 10
142 cm high and 30 cm in diameter were constructed from clear plastic, sunk three
143 centimetres into the sand and sealed with cling-wrap to deter spiderling escape. Four
144 microhabitat treatments were provided within these enclosures; bare soil, veldt grass
145 tufts, *Allocasuarina fraseriana* (Casuarinaceae) and *Banksia attenuata* (Proteaceae)

146 litter. Within each enclosure, configuration of microhabitats was divided into eighths with
147 the two replicate treatments positioned directly opposite one another. An individual
148 spiderling was released in the centre of each enclosure and the location of their burrow
149 recorded on the following day. Chi-square tests were performed for each species using
150 StatistXL v.1.9 to identify microhabitat preference, both in adults and by dispersing
151 spiderlings.
152
153 **Microhabitat characteristics**

154 Ambient temperature (Ta) and relative humidity (RH) was recorded hourly using
155 iButtons in each of the four microhabitat types in the field; bare ground, veldt grass tufts,
156 leaf litter of *A. fraseriana* and leaf litter of *B. attenuata*. Ten iButtons were placed in each
157 microhabitat type at two remnant bushland study sites (Kings Park: 31º57'46.0"S 115
158 º49'52.8"E and Bold Park: 31º56'53.1"S 115º46'13.6"E) and at the spiderling experiment
159 field trial area (32º00'43.1"S 115º53'23.1"E). All iButtons were placed where leaf litter
160 and top layer of soil interacted, except for bare soil microhabitats where iButtons were
161 placed on top of the soil. Records of Ta and RH during 24th May to 6th June 2016 were
162 used for analysis.

163 To assess abundance and diversity of potential prey species, we collected twenty *in situ*
164 ground-cover samples for each of the four microhabitats; ten from Bold Park and ten
165 from Kings Park. Samples were collected within a 20 cm x 20 cm quadrat and were
166 pooled from the same microhabitat and site. Samples were placed in a light-funnel for a
167 week and leaf-litter invertebrates were collected in a jar filled with 100 mL of ethylene-

glycol. These invertebrates were later categorised by size and recognisable taxonomic units (RTUs) (Oliver & Beattie, 1993).

Results

Microhabitat preference

Significant differences in microhabitat preference were found for all three species. Adult microhabitat corresponded with spiderling microhabitat preferences for both *Aganippe* sp. and *I. blackwalli*; spiderlings of these two species preferred open ground cover and *B. attenuata* leaf litter, respectively (Table 1).

Idiosoma sigillatum, a species that typically attaches twig-lines to the rim of their burrow, were predominately found in *A. fraseriana* leaf litter as adults, but selected veldt grass almost exclusively as spiderlings (Table 1). In these cases, no twig-lining was apparent, with one exception where *Allocasuarina* litter from an adjacent treatment was used.

Microhabitat characteristics

A comparison between microhabitat Ta revealed little difference, with all averaging between 14^{o}C and 15^{o}C. Variability in Ta remained most stable in *B. attenuata* leaf litter (range: 23.0, SD: 3.9), followed by veldt grass (range: 23.2, SD: 4.2), *A. fraseriana* leaf litter (range: 23.3, SD: 4.5) and bare ground (range: 26.0, SD: 5.3) (Figure 2).

Relative humidity exposed far greater difference between microhabitats. Leaf litter of *B. attenuata*, leaf litter of *A. fraseriana* and open ground cover all averaged 87.2 - 87.4%.

192 However, a higher RH (93%) was found in veldt grass. Veldt grass retained the most
193 moisture (range: 51.7, SD: 10.5), followed by leaf litter of *B. attenuata* (range: 62.9, SD:
194 12.6), leaf litter of *A. fraseriana* (range: 43.8, SD: 10.6) and open ground (range: 72.2,
195 SD: 15.5) (Figure 3).
196
197 The size of potential prey species varied greatly between microhabitat types. Size
198 classes of 1 mm and 10 mm yielded high numbers (i.e. < 100 individuals) across all
199 microhabitats and can be attributed primarily to two RTUs being Collembola
200 (springtails). Veldt grass yielded the least potential prey in both abundance and species
201 richness (n: 213, S: 10). By comparison, open ground had greater numbers (n: 483) but
202 similar species richness (S: 11) while *Banksia* leaf litter provided more species (S: 21),
203 but lower abundance (n: 393) than open ground. The most productive ground cover was
204 *A. fraseriana* with both highest abundance (n: 6591) and richness (S: 23) (see
205 Supplementary Materials).
206
207 **Discussion**
208
209 Habitat choices consistent with an ecological trap were revealed by *I. sigillatum*
210 spiderlings, as they showed a high preference for invasive veldt grass over native *A.*
211 *fraseriana* leaf litter (where adults were typically found). *Idiosoma sigillatum* spiderlings
212 appeared to have fallen into an ecological trap, as indicated by five factors. Firstly, a
213 high RH in veldt grass may have enticed the spiderlings into this microhabitat. High RH
214 may be an evolutionary trap for this species, as high RH is a physiological requirement

215 for mygalomorphs (Mason *et al.*, 2013). Secondly, *I. sigillatum* is one of a few
216 mygalomorph species in SWA that have a “moustache” twig-line arrangement attached
217 to their burrow rim. This is apparent even as spiderlings when establishing in *A.*
218 *fraseriana* leaf litter. Foraging capabilities may therefore be further compromised when
219 establishing in veldt grass. Thirdly, previous studies have indicated that veldt grass
220 compromises ecosystem functioning (Fisher et al., 2006) and this appears to be
221 supported by our data on low prey species abundance and diversity in veldt grass in
222 comparison to *A. fraseriana*. Fourthly, if, in the wild, *I. sigillatum* spiderlings disperse
223 into veldt grass patches, then there is no evidence they have persisted to adults. Lastly,
224 should spiderlings initially establish in veldt grass and then move, this would result in
225 high energy costs, and leave them vulnerable to predation and desiccation.
226
227 Mygalomorph spiders have exceptionally low fecundity, rendering the probability of
228 locating a brooding mygalomorph spider mother during single surveys very low.
229 Therefore, we were exceptionally fortunate to conduct this study using three individual
230 broods from three species. While there is potential for maternal effects on habitat
231 preference, life history and realised niches of mygalomorph adults suggest a low
232 likelihood of a change in outcome. Our confirmation of mygalomorph spiderling choice
233 in microhabitats is novel. We therefore suggest investigation in other mygalomorph
234 spiders with ready access to brood, such as tarantulas that are routinely used in the pet
235 trade.
236

The impact of invasive grasses effectively transforms and homogenises the ecosystem. By facilitating and interacting with other transforming processes (e.g. nutrient status and fire regime) these grasses form a landscape trap (Fisher, Loneragan, Dixon & Veneklaas, 2009). Reliance on microhabitats, as demonstrated by *Aganippe sp.* and *I. blackwalli*, and other SRE species (Harvey et al., 2011), means that the spread of veldt grass to form a landscape trap is likely to be a threatening process (Figure 4).

As an invasive weed, veldt grass tends to homogenise environments by out-competing native species (Fisher, Loneragan, Dixon & Veneklaas, 2009) and replacing microhabitats. In highly heterogeneous environments that harbour a high diversity of specialist, endemic and co-evolved taxa, homogenisation poses a significant threat to biodiversity (Wardell-Johnson & Horwitz, 1996). Homogenisation of previously heterogeneous habitats is the underlying cause for biodiversity loss worldwide. This has particular significance for the transformation of native habitats through human land-use practices (Sih *et al.*, 2011). In terms of effective management, re-introduction of native species into habitats after a homogenising disturbance would be a poor use of resources (Fisher, Loneragan, Dixon & Veneklaas, 2009). Preventative rather than restorative measures is required (Wardell-Johnson *et al.*, 2016). Restoration is impracticable for the level and time required to rebuild complexity and associated microhabitats (Rebelo et al., 2011). The prevention of likely ecological traps and determination of the circumstances that transform them into landscape traps is imperative for conservation decision-making.

Sedentary taxa enable reliable monitoring of individuals and populations, generating invaluable data for conservation decision-making (Main, 1978). The majority of mygalomorph species exhibit the SRE traits of low mobility, low dispersal, low fecundity, slow growth, restriction to particular habitats, and entire distribution being less than 10 000 km^2 (Harvey, 2002). Some mygalomorph species have capacity to balloon (Pétillon et al., 2012), but this may have evolved to mitigate territorial behaviour (Mason unpublished data) rather than to increase dispersal capability. As such, the biology of particular SRE groups will still need to be considered in management for conservation. Mygalomorphs provide an excellent exemplar of how other SRE may react to novel threatening processes. Unfortunately, exceptionally long lifespan and low reproductive output mean that reduction in fitness, through habitat clearance, disturbance and degradation e.g. through weed invasions, may already be causing localised extinctions in mygalomorphs and other SREs (Rix *et al.*, 2016).

We found invasive veldt grass to be a poor-quality microhabitat compared to native microhabitats. Veldt grass provides an example of ecological and landscape traps in which SRE taxa, such as mygalomorphs, may be caught. In a global context, all specialist species that cannot readily re-locate or adapt are particularly vulnerable to the formation of landscape traps through homogenisation of native microhabitats. While broad-scale management would be ineffective in heterogeneous environments (Wardell-Johnson & Horwitz, 1996), targeting specific, widespread traps, such as weed invasion, may control homogenisation and consequent extinctions.

Conclusion

Informed justification allows cost-effective investment in conservation decision-making. Human-induced rapid environmental change is a significant threat to biodiversity in old, stable landscapes, which are prevalent globally (Mucina & Wardell-Johnson, 2011). Ecosystem functioning will inevitably be compromised and SRE species will go extinct without appropriate conservation management. Identifying potential ecological and landscape traps early will allow us to better manage SREs and other specialist taxa prevalent in heterogeneous habitats. Further studies into the interactions between taxa traits and disturbance will allow more effective management, potentially curtailing impacts of current threatening processes.

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Table 1(on next page)

Microhabitat preferences for three mygalomorph spider species (*Aganippe sp*., *Idiommata blackwalli* and *Idiosoma sigillatum*).

Spiderling preference was recorded under controlled experimental conditions in Perth, south-western Australia. The number of adult burrows found in situ ground cover microhabitats (*Allocasuarina, Banksia*, bare ground, veldt grass) is shown.

Microhabitat preferences for three mygalomorph spider species (*Aganippe sp*., *Idiommata blackwalli* and I*diosoma sigillatum*). Spiderling preference was recorded under controlled experimental conditions in Perth, south-western Australia. The number of adult burrows found in situ ground cover microhabitats (*Allocasuarina, Banksia*, bare ground, veldt grass) is shown.

	Species	*Allocasuarina*	*Banksia*	Bare ground	Veldt grass	n	d.f.	p value
Spiderlings	*Aganippe sp.*	8	12	21	9	50	3	0.04
	Idiommata blackwalli	3	11	3	3	20	3	0.01
	Idiosoma sigillatum	2	0	0	38	40	3	< 0.001
Adults	*Aganippe sp.*	1	2	10	0	13	3	< 0.001
	Idiommata blackwalli	3	15	0	0	18	3	< 0.001
	Idiosoma sigillatum	17	4	4	0	25	3	< 0.001

Figure 1

Subject spider species and their burrows.

Three species of mygalomorph spider used in the study and their corresponding burrows; a) *Idiosoma sigillatum*, b) *Idiomatta blackwalli* and c) *Aganippe sp*. Scale bars in the bottom right corner of burrow photos refers to the widest point across the burrow entrance. All three species occur within patches of urban bushland within Perth, Western Australia. Photo credits: Bill Bateman for Aganippe sp. spider, Jessica Moran for Idiommata blackwalli spider and Leanda Denise Mason for all others.

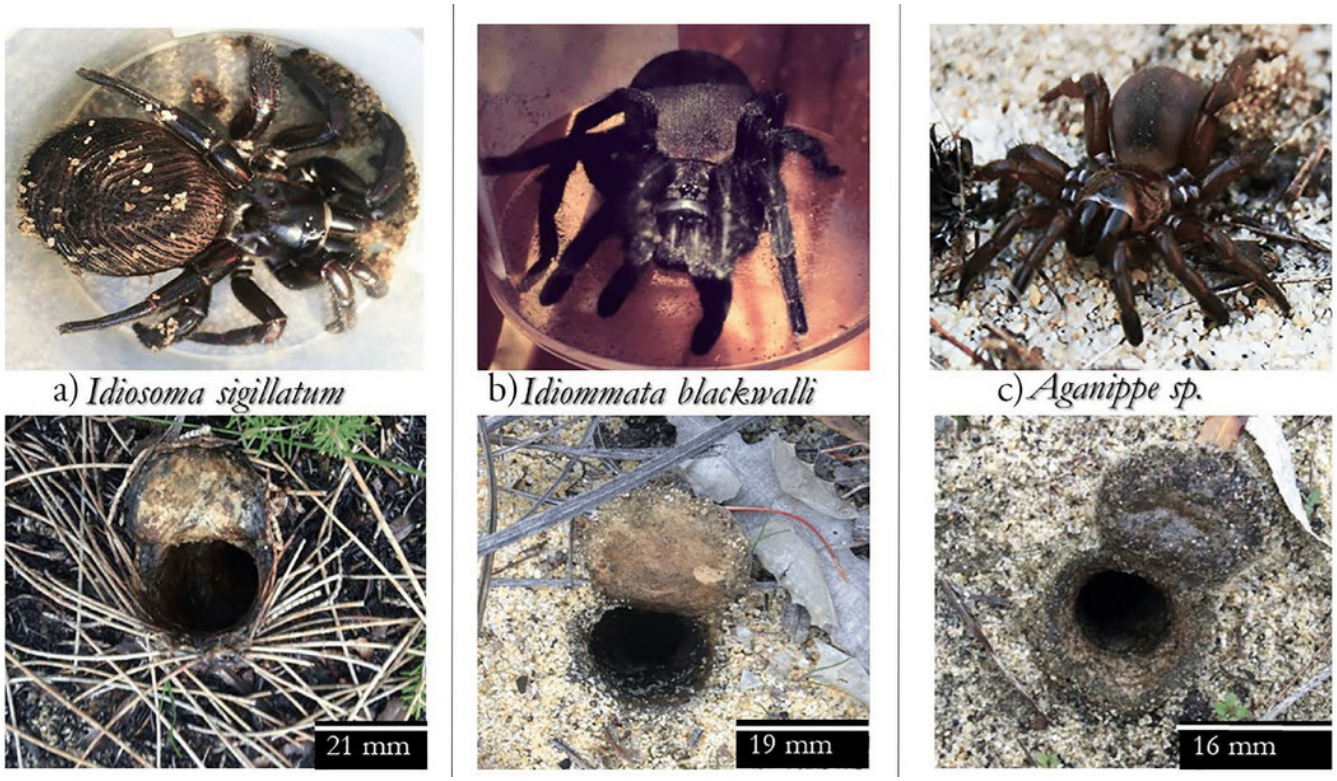


Figure 2

Ambient temperature fluctuation in microhabitats

A box-and-whisker plot comparing the differences in ambient temperature (C°) fluctuation during 24th May – 6th June, 2016 in different ground cover types (*Banksia* leaf and *Allocasuarina* leaf litter, bare ground and veldt grass) found in urban bushland of Perth, Western Australia.

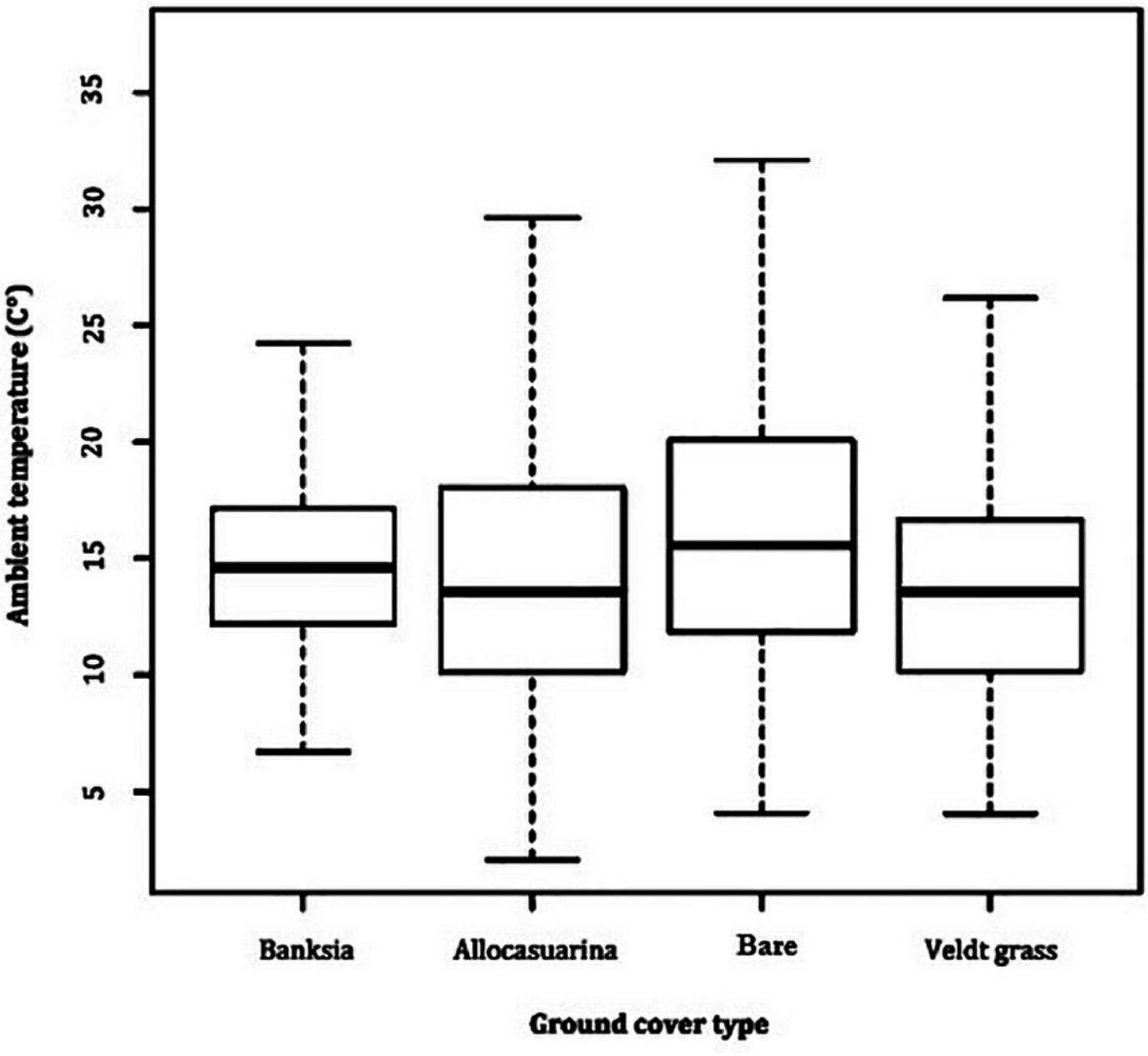


Figure 3

Relative humidity fluctuations in different microhabitats

A box-and-whisker plot comparing the differences in relative humidity (%) fluctuation during 24th May – 6th June, 2016 in different ground cover types (*Banksia* leaf and *Allocasuarina* leaf litter, bare ground and veldt grass) found in urban bushland of Perth, Western Australia.

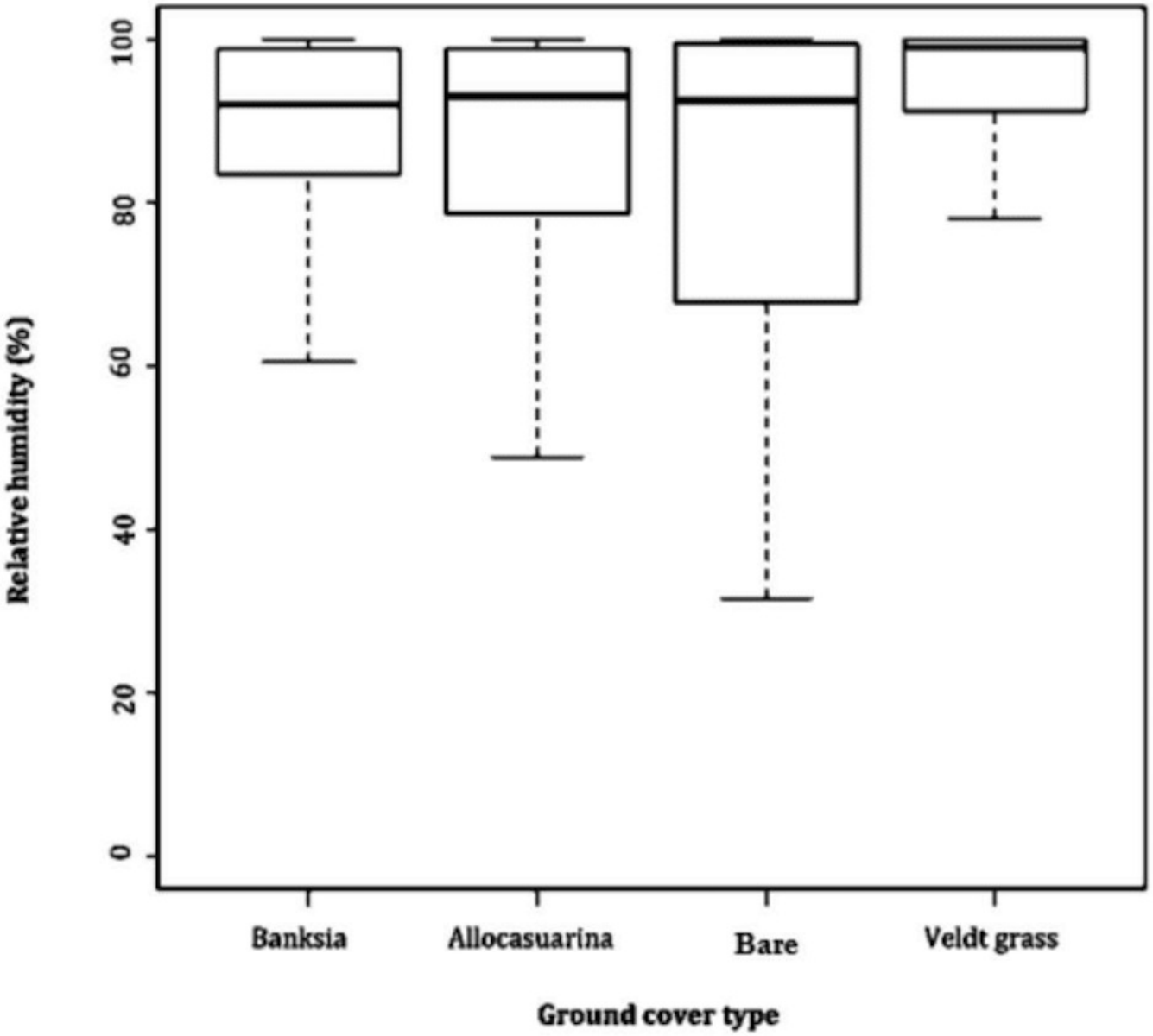
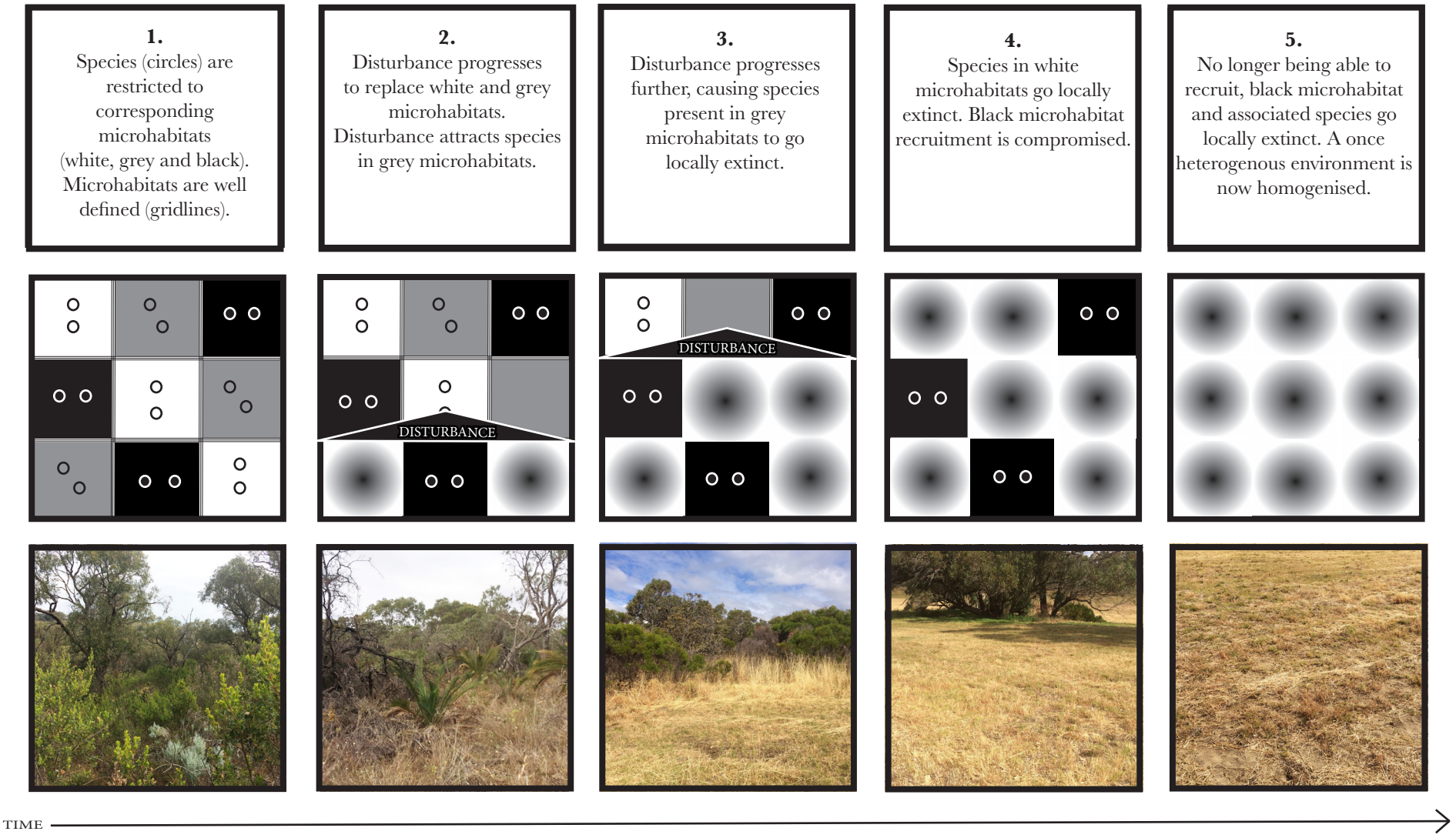


Figure 4(on next page)

Short-range endemics get caught in ecological and landscape traps

Hypothetical representation of short-range endemic species in response to ecological traps and landscape traps over time. The example, including all photographs, is from Bold Park in Perth metropolitan area of Western Australia. Photo credit: Leanda Denise Mason.


1.
Species (circles) are restricted to corresponding microhabitats (white, grey and black). Microhabitats are well defined (gridlines).
2.
Disturbance progresses to replace white and grey microhabitats. Disturbance attracts species in grey microhabitats.
3.
Disturbance progresses further, causing species present in grey microhabitats to go locally extinct.
4.
Species in white microhabitats go locally extinct. Black microhabitat recruitment is compromised.
5.
No longer being able to recruit, black microhabitat and associated species go locally extinct. A once heterogenous environment is now homogenised.
DISTURBANCE
DISTURBANCE
TIME