Layers of contingency shroud pervasive ecological divergence in a local radiation of land snails

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The predictability of evolution depends on the roles that selection and historical contingency play in determining its outcomes, but the relative importance of these evolutionary mechanisms has attracted considerable debate. One view is that historical events have such a profound impact on the genetic structure of populations that patterns of phenotypic evolution are essentially unpredictable. The opposing view is that selection is so powerful that evolutionary change is primarily deterministic, and thus highly predictable. By controlling for the effects of phylogeny, geographic location and habitat, this study examined the relative roles of contingency and determinism in a local radiation of land snails, genus *Rhagada*, in a continental archipelago. Informed by previous studies on a single island, which revealed a strong association between low-spired shells and rocky habitats, 28 population pairs were sampled in directly adjoining rocky and spinifex plain habitats. When considered in their respective pairs, the effect of habitat was remarkably consistent, with lower-spired shells observed in the rocky habitat in 24 of the comparisons. However, when analyzed outside the context of those pairs, the association was obscured by broad variation in shell shape within habitat types and among lineages. These results reveal the complex nature of a morphological radiation; while the pattern of ecological divergence is highly predictable at the scale that selection acts, deterministic evolution is largely obscured by phylogenetic and population history. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **00**, 000–000.

ADDITIONAL KEYWORDS: adaptation – constraint – determinism – history – *Rhagada* – selection – shell shape.

INTRODUCTION

The predictability of evolution depends on the roles that selection and historical contingency play in determining its outcomes (Losos, 2010, 2011), but the relative importance of these evolutionary mechanisms has attracted considerable debate (Lewontin, 1966; Gould 1989; Travisano *et al.*, 1995; Losos *et al.*, 1998; Blount, Borland & Lenski, 2008). Some authors have argued that the contingencies of history are so influential in determining genetic structure, that evolutionary change is essentially unpredictable (Gould 1989). Others have argued the polar opposite view, suggesting that selection is a powerful deterministic force that regularly overcomes the contingencies of history, resulting in convergent, and thus predictable, evolutionary outcomes (Losos *et al.*, 1998).

These diametrically opposing views surrounding the predictability of phenotypic evolution stem, in part, from how convergence is defined (Losos, 2011). When defined as the independent evolution of identical or very similar phenotypes among replicated environments, studies will only detect convergence if there is a tight relationship between phenotype and environment. Although some clear and striking examples of convergent morphological radiations are known (Losos *et al.*, 1998; Chiba, 2004), many studies report non-convergent evolutionary patterns, suggesting that evolution is neither deterministic nor predictable (Losos, 2010, 2011). The issue with this approach is that complex phenotypes are inherently contingent. Although deterministic evolution may be driving independent populations towards the same phenotypic or

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functional optima, historical contingencies may affect the progress and passage of evolutionary change. Thus, phenotypes may be best viewed as local, temporary solutions to a selective problem rather than evidence against deterministic evolutionary change. Consistent with this view, studies that have defined convergence based on trajectory of phenotypic or functional evolution have shown that evolution is highly deterministic, and that the evolutionary outcomes are often highly replicable and predictable (Young, Snoeks & Seehausen, 2009; Losos, 2011; Ożgo, 2011).

This study focuses on the predictability of evolutionary outcomes in a diverse group of land snails, genus *Rhagada*, in northwestern Australia's Dampier Archipelago. While morphologically conservative over the majority of its 200 000 km^2 mainland distribution, *Rhagada* in the Dampier Archipelago has unusually diverse shell morphologies, with variation in size, shape, sculpture and banding pattern that spans the range of variation in the entire genus (Johnson *et al.*, 2012; Stankowski & Johnson, 2014). Although this variation was thought to represent distinct, widespread species, phylogenetic studies of mitochondrial DNA indicate that very similar shell forms have evolved several times throughout the archipelago during a recent morphological radiation (Stankowski & Johnson, 2014). The radiation involves three divergent clades, two of which are endemic to the Dampier Archipelago (Clades C and D), while the third occupies the islands and the adjacent mainland (clade A; Johnson *et al.*, 2012). Most of the phenotypic variation occurs within one of the endemic clades, clade D, which is further subdivided into five mitochondrial subclades, and is the most widespread in the archipelago (Stankowski & Johnson, 2014). While it is clear that much of the variation in the Dampier Archipelago *Rhagada* reflects local evolution, it is not clear whether the divergence reflects spatial variation in the pattern of current selection, or has evolved as a consequence of the unique histories experienced by lineages or populations (Stankowski & Johnson, 2014).

Shell shape has, however, been studied in detail on a single island, Rosemary Island, in very closely related groups of populations whose shells range from globose to flat-spired, spanning the entire range of variation in the genus (Stankowski, 2011, 2013). On that island, there is a clear, repeated association between shell shape and habitat. Keeled-flat populations inhabit two rocky hilltops, while the taller, globose-shelled populations occupy the surrounding spinifex plains. Despite the range of morphological variation, microsatellite DNA has provided direct evidence for gene flow between the strongly divergent forms which hybridize at a narrow ecotone between the contrasting environments (Stankowski, 2013). Detailed analysis of mitochondrial DNA on the island provided no evidence for a role of historical isolation in the evolution or maintenance of the geographic variation. Instead, there is strong evidence that the variation evolved *in situ* due to strong, divergent selection favouring the different shell shapes in their respective environments in the face of gene flow (Stankowski, 2013).

This investigation tests the generality of the hypothesis developed from *Rhagada* on Rosemary Island, taking advantage of the natural replication of the same contrasting environments throughout the Dampier Archipelago. By using locally paired populations to control for habitat, phylogeny and geographic position, three specific questions are addressed. First, is there a consistent association between flatter shells and rocky habitats among the pairs, permitting the prediction of the relative shape of shells? Second, is the extent of divergence consistent among the pairs, so that absolute shape of shells can be predicted from the local habitat? Third, what are the relative contributions of selection, phylogenetic history and population history to the geographic pattern of shell shape in the Dampier Archipelago, and at what scale is each force most important?

MATERIAL AND METHODS

SAMPLES

According to the existing taxonomy for the genus (Solem, 1997) and more recent surveys of the islands (Johnson *et al.*, 2012), seven described and three putative species of *Rhagada* are recognized in the Dampier Archipelago. However, a detailed phylogenetic analysis, including specimens from all the recognized forms, provided no support for the shell-based taxonomy of the island endemic species (Stankowski & Johnson, 2014). Thus, with the exception of the primarily mainland species *Rhagada convicta*, which has only a marginal distribution in the Dampier Archipelago (Johnson *et al.*, 2012; Stankowski & Johnson, 2014), specimens are referred to based on their associated phylogenetic clade rather than the existing taxonomic names (Fig. 1).

Twenty-eight independent pairs of sample sites were examined in directly adjoining rocky and spinifex plain habitats across nine islands in the Dampier Archipelago (Fig. 1). Each pair was selected using five criteria, designed to minimize the variation in the contingent histories experienced by paired populations and maximize the possibility of detecting local adaptive divergence. Paired populations were always: (1) from the same phylogenetic clade, as revealed in Stankowski & Johnson (2014), (2) from
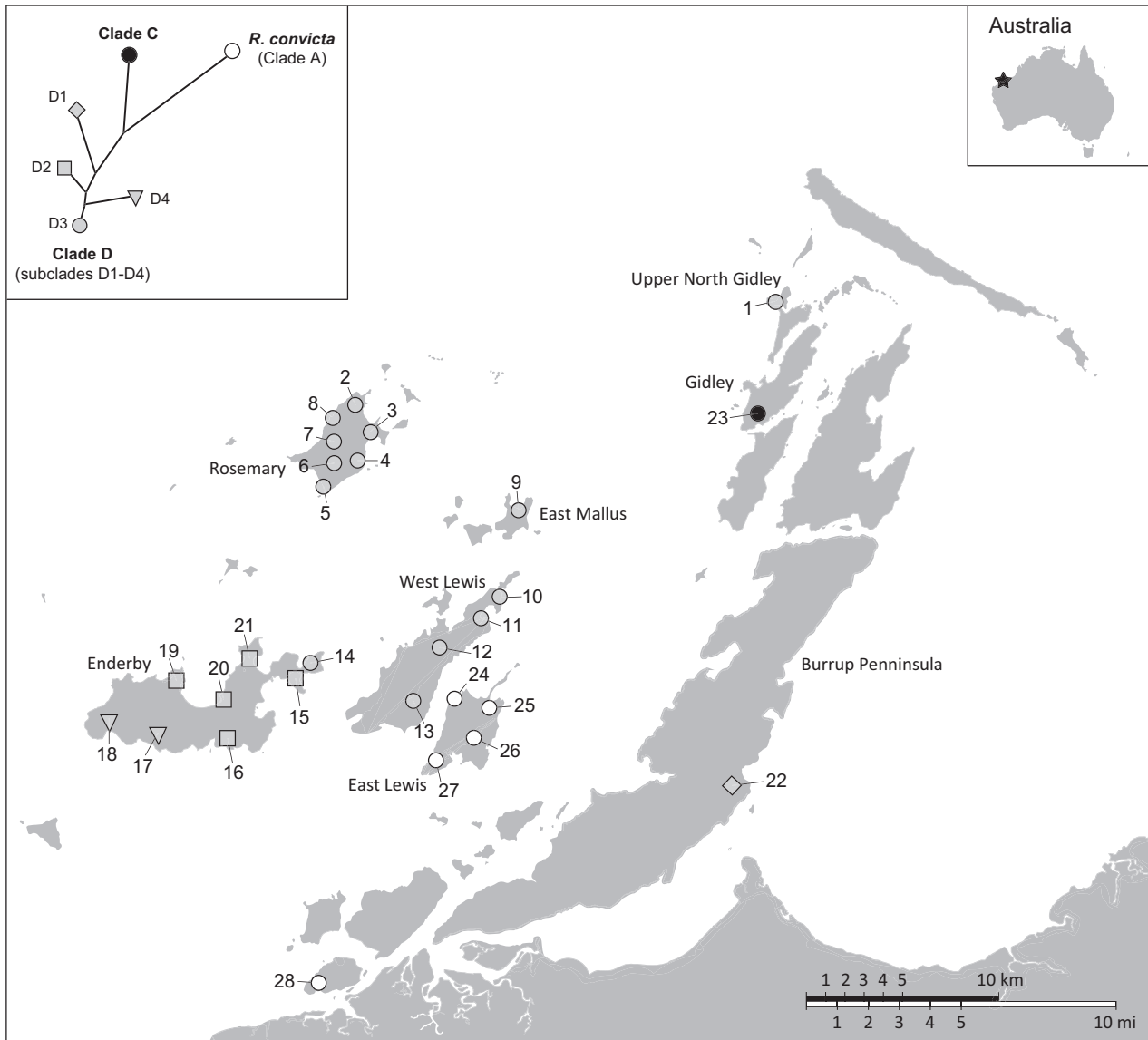
Figure 1. Locations of the 28 population pairs. Each symbol represents two sample sites established in directly adjoining spinifex plain and rocky habitats. Symbol shape indicates mitochondrial clade of origin, shown in the unrooted network (top left). The three major clades (A, C, D) observed in Johnson *et al.* (2012) are distinguished by shading.

the same island, and (3) separated by no more than 1000 m of continuous habitat. In addition, (4) paired populations were separated by no less than 150 m, because gene flow between contrasting habitats has been shown to disrupt local adaptation over that scale (Stankowski, 2013). For the same reason, (5) the alternative habitat patches were at least 280 m wide, which is an area larger than the smallest rocky hill where local divergence has been documented (Stankowski, 2013).

Up to 20 live adult *Rhagada* were collected at each of the 56 sampling locations, distinguished from juveniles by the presence of a reflected lip at the

shell aperture, which marks the cessation of shell growth (Solem, 1997). When unable to collect a full sample of live adults, empty adult shells were included, with preference towards those with 'live' colour and texture. In almost all cases, the material at each site was collected within a 15 m radius, which is smaller than the neighbourhood size estimated for the *R. capensis* (Johnson & Black, 1991).

MOLECULAR DIVERGENCE WITHIN AND AMONG PAIRS

The main aim of the paired design is to minimize the different historical conditions experienced by populations

in contrasting habitats. To confirm that the paired populations have shared close histories, a 633-bp fragment of the rapidly evolving mitochondrial gene cytochrome oxidase I (*COI*) was amplified from up to six individuals per location according to Stankowski & Johnson (2014). Sequences were edited and aligned with SEQUENCHER v.4.6, and MEGA version 4 (Tamura *et al.*, 2011) was used to calculate estimates of pairwise distance (*P*-distance) between them. Separate frequency-distributions histograms were produced from the results of the within- and among-pair comparisons. GenBank accession numbers are provided in the Supporting Information (Table S1).

ESTIMATES OF SHELL SHAPE

A previous study of *Rhagada* form one island in the Dampier Archipelago used geometric morphometric analysis to quantify variation in relative shell height (Stankowski, 2011). However, linear measurements of the same set of samples produced near identical estimates of shell shape ($r^2 = 0.98$). Here, size-corrected estimates of relative shell height were obtained form linear measurements as the residuals of the regression of shell height on shell diameter. Although the analysis of data was limited to the 56 focal populations, the estimates of relative shell height were made within the context of the more extensive samples examined in Stankowski & Johnson (2014). Estimates of shell height and width were thus obtained for 2256 adult shells from 173 sample sites according to Cain (1977), using digital calipers accurate to 0.01 mm. The standard deviation of shell measurements, as determined by the repeated measurement of single specimens, was approximately 0.02 mm. Two different estimates of shell shape were obtained for each specimen. The first, referred to as the 'global' shape score, was obtained from a regression performed on the entire sample of 2256 measured shells. Because different phylogenetic groups may have their own unique height/diameter scaling relationships, 'clade-specific' shape scores were also obtained for each specimen by performing separate regressions for each mitochondrial clade revealed in Stankowski & Johnson (2014). Mean global and clade-specific shape scores were obtained for each of the 56 focal populations used to test for an effect of habitat on shape.

EFFECT OF HABITAT ON SHAPE

As the data did not meet the assumptions of parametric analysis, four separate non-parametric Wilcoxon tests, conducted in SPSS v.11 (IBM corporation, Armonk, NY, USA), were used to test for an effect of habitat on shell shape. The first test, an independent-samples Wilcoxon test, was conducted on mean population global shape scores, to test for an effect of habitat, independent of the spatial proximity and phylogenetic history of populations. The second test, also an independent-samples Wilcoxon test, was conducted on mean clade-specific shape scores to correct for the effect of phylogeny on shape. The third and fourth tests were paired-samples Wilcoxon tests, both taking advantage of the paired sampling design. The third test was conducted on mean global shape scores, and thus provided a test for the effects of habitat on shape, correcting for the effect of spatial proximity. The fourth test was conducted on mean clade-specific scores, providing a test for the effects of habitat on shape while correcting for the effects of spatial position and phylogeny.

Exact binomial tests, implemented in JMP v.5 (SAS institute inc., Cary, NC, USA), were then used to test for a general effect of habitat on shape, ignoring the magnitude of the effect, but taking the effects of phylogeny and spatial proximity into account. The test calculates the exact probability of obtaining *n* type 1 observations based on the number of type 1 and type 2 observations obtained from *N* observations, assuming that the probability of observing type 1 and type 2 events is equal. Here, each pair was classified as either positive or negative, based on whether the rocky site had a higher or lower mean clade-specific shape score, respectively. A Fisher's exact test for a 2×2 contingency table was then used to compare the proportion of positive and negative responses between the island endemic lineage (clades D1–D4 in Fig. 2) and the primarily mainland species, *R. convicta* (clade A). The third major lineage (clade C), also endemic to the Dampier Archipelago, was excluded from this analysis because it was represented by a single habitat pair.

RESULTS

MOLECULAR VARIATION WITHIN AND AMONG PAIRS

The analysis of COI sequences confirmed the close relationships between the populations within each of the 28 pairs (Fig. 2). Within the entire sample, estimates of uncorrected pairwise distances ranged from 0 to 17.9%, with a mean value of 6.64% ± SD 4.74. The distribution of scores was trimodal, with local peaks at 5, 9 and 13% divergence. Pairwise distances calculated among population pairs had the same range of divergence scores, though the mean distance was slightly higher at 6.83% ± SD 4.71. In contrast, distances within pairs were much lower, ranging from 0% to 6.45% ± SD 1.33, with a mean of 1.33%. Rather than consisting of several local peaks, the
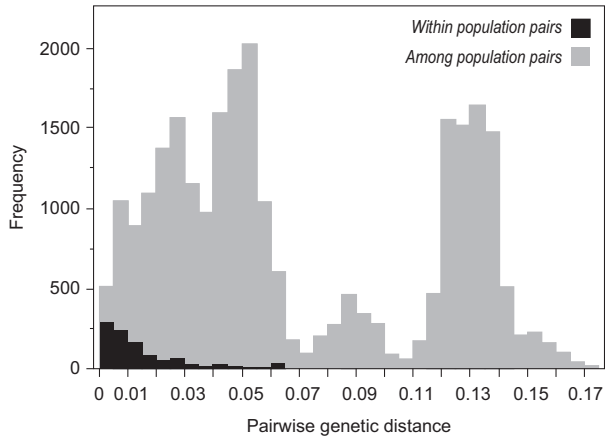
Figure 2. Frequency-distribution of pairwise distances among COI haplotypes from the 56 sample sites. The grey areas of the histogram represent comparisons made among pairs, while the black areas represent comparisons made within population pairs.

distribution of distances within pairs was positively skewed, with the majority of estimates falling between 0 and 1%, and decayed rapidly as pairwise distance increased.

GLOBAL AND CLADE-SPECIFIC ESTIMATES OF SHELL SHAPE

Regression analysis revealed a strong relationship between shell diameter and shell height within the global sample of 2256 shells ($r^2 = 0.88$; $P < 0.0001$; Fig. 3, left). For each unit increase in shell diameter, shell height increased by 0.89. Despite the strength of the relationship, there was considerable residual variation in shell height, ranging from 3.44 to −6.92 mm. Mean residual scores obtained for the 56 focal populations ranged from 1.33 mm ± SE 0.23 to −5.79 mm ± SE 0.11.

Additional regression analyses revealed striking heterogeneity in the scaling relationships between shell height and shell diameter among the six clades (Fig. 3, right). In all cases, the rate of change in shell height was less than that of shell diameter, but there was considerable variation in the slope and intercept among clades. Mean clade-specific scores obtained for the focal populations spanned a similar range to those obtained from the global analysis (0.98 mm ± SE 0.09 to −6.06 mm ± SE 0.11). However, plotting the global and clade-specific population estimates of residual height against one another revealed considerable discrepancy between the different estimates of shell shape (Fig. 4, right). The absolute difference between the estimates ranged from 0.036 to 1.94 mm, with a mean of 0.496 mm ± SD 0.417.

EFFECT OF HABITAT ON SHELL SHAPE

There was broad overlap in global and clade-specific shape scores between rock-dwelling and spinifex plain populations (Fig. 4). The mean global estimate of shape was higher in the spinifex plain habitat (0.321 mm ± SE 0.11) than in the rocky habitat (−0.451 mm ± SE 0.317), although an independent-samples Wilcoxon test revealed that the difference was only marginally statistically significant ($Z = -1.950$, $P = 0.0511$; Table 1). When the same test was conducted on the clade-specific shape scores, the difference was clearer ($Z = -2.261$; $P = 0.0237$), with mean estimates of 0.212 mm ± SE 0.841 and −0.677 mm ± SE 0.264 for spinifex plain and rock-dwelling populations, respectively.

When populations were considered in their respective pairs, the effects of habitat were much clearer (Table 1). Based on paired Wilcoxon tests, comparing either global or clade-specific scores, the difference in shape between habitats was highly significant. However, statistical confidence was a full order of magnitude higher in the test that was based on clade-specific shape scores ($Z = -3.461$; $P = 0.0005$) than that which compared global scores ($Z = -2.710$; $P = 0.0067$). The consistent effect of habitat on shape was revealed most clearly by the analysis of the direction of the difference in residual shell height scores within each pair (Fig. 5). Based on the clade-specific estimates of shape, populations in rocky habitat had flatter shells in 24 of the 28 pairs. Under the null hypothesis of no effect of habitat on shape, the probability of obtaining the 24 responses in the same direction is 0.0004. Of the four pairs that showed the opposite trend, only one pair was from the widespread endemic Dampier Archipelago lineage, represented by a total of 23 pairs, while the other three were three of the four population pairs of *R. convicta* (Lineage A), the predominately mainland species. Based on a Fisher's exact test of a 2 × 2 contingency table, this difference in the proportions of positive and negative responses of the two groups was significant ($P = 0.0047$).

DISCUSSION

By controlling for the effects of habitat, phylogeny and spatial proximity at different stages of the analysis, this study attempted to understand the relative importance of selective and historical processes in the evolution of shell shape within a single genus. The results indicate that both mechanisms have played an important role in the evolution of the observed pattern, though the dominant force varies with scale. At the finest spatial and evolutionary
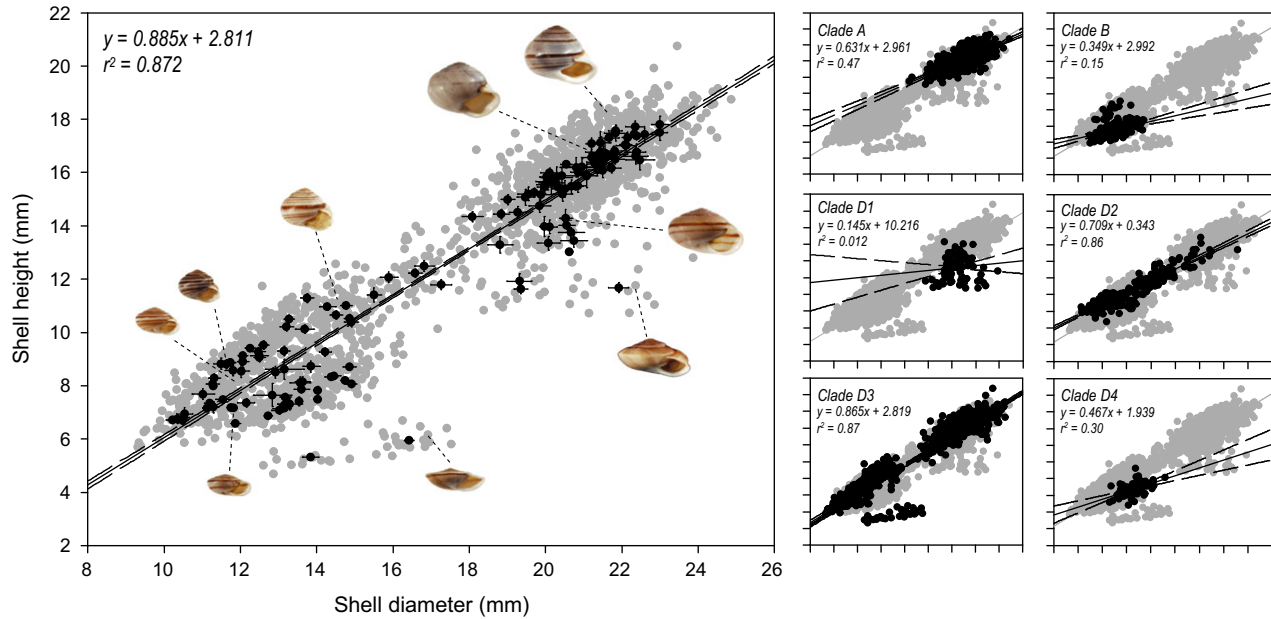
Figure 3. Bivariate scaling relationships between shell width and shell height. The main plot shows the least-squares linear regression of height on width for the entire sample of shells ($N = 2250$), along with representative images of each of the described and putative species. The grey points are the individual scores. The black points are the mean estimates for each sample site; the horizontal and vertical lines represent the standard errors of the means for shell width and height, respectively. The dashed line represent the 95% confidence interval for the regression. The six plots on the left plots show the scaling relationships for each phylogenetic clade.

scale, within the population pairs, the pattern of divergence is highly predictable, with flatter-shelled *Rhagada* observed in the rocky habitat in 24 of the 28 pairs. Within each pair, the populations are very closely related to one another, and are connected by continuous habitat, so are also likely to be connected by gene flow, as has been demonstrated between the globose and flat-spired populations on Rosemary Island (Stankowski, 2013). Thus, while spatial variation can evolve at this scale as a result of drift or population history, the consistent pattern suggests that selection has favoured different shaped shells in these contrasting environments.

In addition to the populations on Rosemary Island (Stankowski, 2013), where the role of divergent environmental selection is exceptionally clear, several other studies have reported an association between low-spired populations and rocky habitats (Goodfriend, 1986; Teshima *et al.*, 2003; Haase & Misof 2009; Moreno-Rueda, 2009; Haase *et al.* 2013) and in intertidal snails (Johnson & Black, 2000). Of the potential mechanisms that have been suggested to explain the evolution of flatter shells, two seem most likely to be driving the evolution of shape in these populations. First, it is possible that flatter shells have evolved as an adaptive response to variation in the available refuge sites. The Dampier Archipelago

has a hot, arid climate, which is characterized by low, unreliable rainfall. To avoid desiccation, *Rhagada* in the spinifex plain habitat burrow into the soil at the base of the plants, where they aestivate for most of the year (Solem, 1997). In rocky habitats, where soil is shallow or scarce, snails are most often found under rocks or in narrow rock crevices that could not be accessed by snails with taller shells. Second, the variation in shape between habitats may reflect a trade-off between shell stability during locomotion and available space for a soft body (Okajima & Chiba, 2009; Noshita, Asami & Ubukata, 2012; Hirano *et al.*, 2015). In rocky habitats, where a large proportion of the substrate is vertical, lower-spired shells are theoretically better balanced during locomotion, requiring less energy to carry, than are taller globose-shaped shells (Okajima & Chiba, 2009). In the spinifex plain habitat, however, where very little part of the habitat is vertical, the flatter shape would confer little advantage during locomotion, but would constrain the animal's body size. Further work is required to understand the mechanism(s) underlying the associations between shape and habitat in the Dampier Archipelago.

Four pairs of populations showed the reverse trend with habitat, with flatter-shelled populations observed in the spinifex plain habitat. Three of these
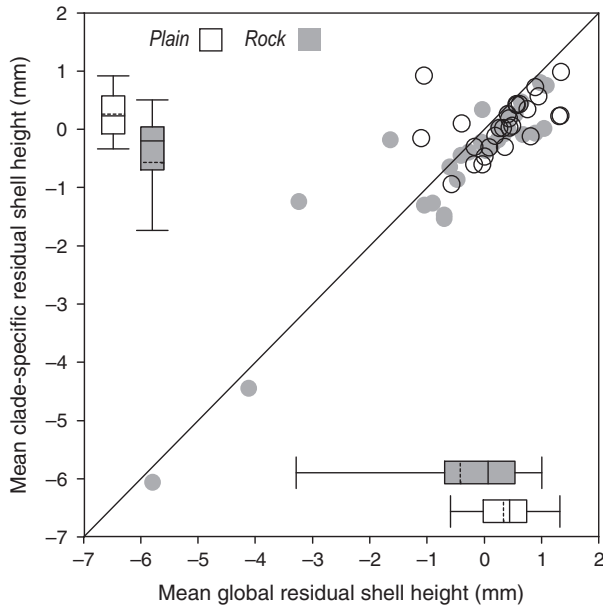
Figure 4. Mean clade-specific and mean global shell height scores for the 56 focal populations. Filled circles represent populations in rocky habitat, while the open circles represent population in the spinifex plain habitat. The box plots associated with each axis show mean (dashed line), median (solid line), 25th and 75th percentile (lower and upper boundaries of the box) the 10th and 90th percentile values in each habitat type.

Table 1. Results of non-parametric Wilcoxon tests comparing population estimates of shell shape between habitat types

Design	Z	P
Unpaired, global scores	−1.950	0.0511
Unpaired, clade-specific scores	−2.261	0.0237
Paired, global scores	−2.710	0.0067
Paired, clade-specific scores	−3.461	0.0005

pairs consisted of populations of the species *Rhagada convicta* (clade A), which is deeply divergent from the other *Rhagada* that inhabit the Dampier Archipelago (Hamilton & Johnson, 2015). This result is interesting for three reasons. First, *R. convicta* has a large mainland distribution and only a marginal distribution in the Dampier Archipelago (Hamilton & Johnson, 2015). Rocky habitats are rare throughout its mainland distribution, where *R. convicta* is almost exclusively associated with sandy spinifex plains (Johnson *et al.*, 2012). Second, within the Dampier Archipelago, this species rarely occupies rocky areas, despite having many opportunities to do so (personal observation). Third, *R. convicta* is depauperate of morphological

variation compared with the diverse clade D, suggesting that *R. convicta* may lack the variation required to exploit the rocky habitats that exist only on the edge of its geographic range. Together, these observations suggest that phylogenetic history is important in determining how populations respond to variation in habitat in the Dampier Archipelago.

Although the direction of phenotypic divergence is highly consistent within the pairs from the island endemic clade D, there is considerable overlap of shape scores between the habitat types. Consequently it is not possible to predict the absolute shape of shells based simply on knowledge of the habitat, even in this geographically and genetically closely related group. The evolution of non-convergent phenotypes among replicated habitats has classically been interpreted as evidence against the importance of ecological selection in the evolutionary process (Young *et al.*, 2009; Losos, 2011). However, recent studies that have combined analyses at both 'global' and 'local' scales have revealed evidence for phenotypic non-convergence at the broad scale, but clear evidence for parallel ecological divergence at the scale that deterministic selection is expected to act. For example, in a study of the polymorphic snail *Cepaea nemoralis* in Eastern Europe, Ożgo (2011) studied 12 independent population pairs in directly adjoining open and shaded habitats. Within 10 of the 12 pairs, there was a transition towards darker, more banded shells within the shaded habitat, an observation that is consistent with studies of British populations (Cain & Sheppard, 1954). However, when analyzed outside the context of those pairs, there was no clear association between habitat and shell colour or banding pattern. Similarly, a study of independent radiations of cichlid fish in three of Africa's Great Rift Lakes by Young *et al.* (2009) found that, when analyzed in a common morphospace, ecological equivalents from different lakes differed from one another on the basis of their shape. However, within each radiation, the different ecotypes had diverged from one another along the same morphological axis in all three cases.

As with the above examples, there are a limited number of explanations for the non-convergence of form within habitat types in *Rhagada*. One possibility is that the broad-scale non-convergence has evolved due to cryptic variation in the selective environment. That is, while the replicated environments may be superficially similar, the selective environment may actually be quite different. The common selective agents may vary in strength among locations, and other selective agents, unique to specific locations, may constrain the pattern of evolution along certain morphological axes. While such a selective explanation cannot be ruled out, historical
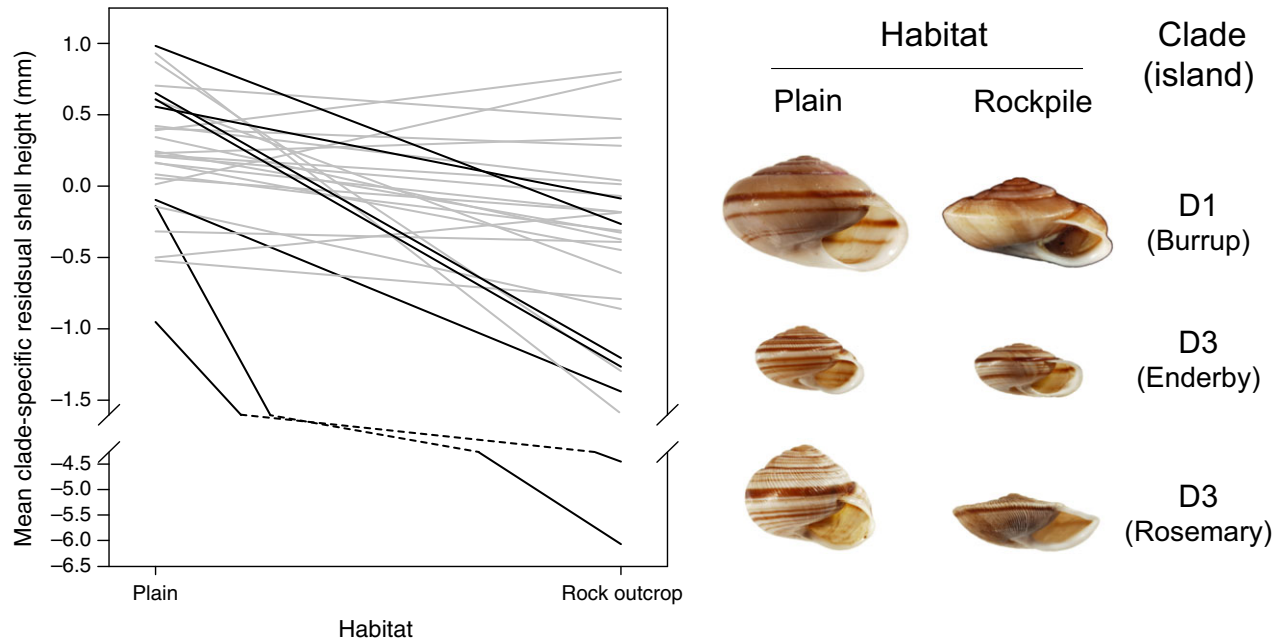
Figure 5. Variation in shell shape (mean clade-specific residual shell height) within and among paired habitat contrasts, along with representative photographs of shells from three population pairs. Each line connects a pair of populations in adjacent, contrasting habitats. The black lines represent pairs from Rosemary Island; the two flattest rock-dwelling populations studied in Stankowski (2013). The dashed sections of line pass through the break in the y axis.

contingency has probably played a primary role in the broad-scale patterns. While it is possible only to speculate as to what the historical events leading to the differences may have been, the effects of history are clear at two levels, the deepest being phylogenetic history. The clade-specific height to width scaling relationships show that some clades differ remarkably in their shape even before the effects of habitat are considered. The effects of local population history are also clear. Even within clades, populations vary dramatically in their shape scores, for the most part, independent of the local habitat. This pattern is clear on Rosemary Island, where there are seven closely related population pairs that span the full range of shape in the genus. When considered outside their pairs, much of the variation in shell shape is independent of habitat, though within pairs, rock-dwelling populations always have flatter shells.

Variation in local population history has almost certainly played some role in determining the pattern of variation within the clades. Sampling drift or demographic events can reduce levels of variation in populations, limiting their potential to adapt. Mutations would introduce variation into populations at random, so that some populations may have acquired the variation needed to evolve lower-spired shells, while others have not. The rocky areas are

discrete pieces of environment imbedded in a matrix of contrasting low-lying habitat. Studies of hybrid zones between the derived, flat-spired and ancestral, globose-shelled populations on Rosemary Island suggest that the functional genetic variation contributing to flatter shells may have evolved locally, and may be largely trapped on each rocky hill by strong divergent environmental selection (Stankowski, 2013). Thus, the distribution of phenotypes in the Dampier Archipelago may depend more on chance than on the spatial variation in the pattern of selection.

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SUPPORTING INFORMATION

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

Table S1. Sample site information and GenBank accession numbers for populations examined in the study.