Using connectivity to identify climatic drivers of local adaptation

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Abstract

Despite being able to conclusively demonstrate local adaptation, we are still often unable to objectively determine the climatic drivers of local adaptation. Given the rapid rate of global change, understanding the climatic drivers of local adaptation is vital. Not only will this tell us which climate axes matter most to population fitness, but such knowledge is critical to inform management strategies such as translocation and targeted gene flow. Targeted gene flow, for example, requires knowledge of where in the landscape we can find populations with pre-adapted climate-relevant traits; we cannot find these populations if we do not know the dominant climatic drivers of local adaptation. While simple assessments of geographic trait variation are useful, geographic variation — and its associations with environment — may represent plastic, rather than evolved differences. Additionally, the vast number of environment–trait combinations makes it difficult to determine which aspects of the environment populations adapt to. Here we argue that by incorporating a measure of landscape connectivity as a proxy for gene flow, we can differentiate between environment–trait relationships that are under selection versus those that reflect phenotypic plasticity. By doing so, we can rapidly shorten the list of environment–trait combinations that may be of adaptive significance. We demonstrate this method using data on geographic trait variation in a lizard species from Australia's Wet Tropics rainforest.

Significance Statement

Despite 150 years of evolutionary research, we still do not have a good method for determining the climatic drivers of local adaptation. Having such a method is critical if we are to understand and mitigate the impact of climate change. Here we exploit the fact that local adaptation is eroded by gene flow to develop a new method for identifying the environmental drivers of local adaptation. Our method will allow workers around the world, for the first time (and often using existing datasets), to determine the climatic drivers of local adaptation in their system. As such, the method has powerful implications not only for pure evolutionary research, but also for management.

Introduction

It is only recently that we have begun to appreciate the speed with which evolution can happen; not only over relatively short timespans (e.g., 1, 2-4), but also at small spatial scales (5). Rapid local adaptation has been recorded in response to a wide suite of environmental drivers, including invasive species, and pollution (6). We expect climate to also be a major driver of local adaptation (e.g., 7, 8), and understanding the way in which species respond to climate is of increasing importance because anthropogenic climate change is proceeding at such a rate that there are concerns that many species will be unable to evolve rapidly enough to avoid extinction (9, 10).

Evolution typically optimizes phenotypes, but the optimum will vary through both time and space (11, 12), in turn leading to populations ('demes') that have, on average, higher fitness in their home environment than an immigrant would: local adaptation. While adaptive optima for traits almost always vary geographically, it does not follow that all geographic trait variation is due to local adaptation. Geographic trait variation can arise due to other factors, such as phenotypic plasticity (including developmental plasticity and maternal effects) and environmental factors (such as geographic variation in fitness-reducing parasites). These factors, and particularly phenotypic plasticity, can give the appearance of local adaptation, despite having no underlying heritable basis (10, 11), complicating our identification of climate-relevant adaptive variation.

To circumvent these issues, evolutionary biologists use experimental approaches to demonstrate local adaptation (12, 13). Experiments designed to detect local adaptation typically utilise one of two techniques: 1) reciprocal transplants, which are done *in*

situ, and are considered the gold standard for demonstrating local adaptation; or 2) common garden experiments, which are usually done in the lab where it is easier to control each environmental variable (12). Both of these techniques can be difficult, for reasons of time, expense, logistics, or ethics. This difficulty increases as the number of separate demes and environmental variables to be tested increases and as the generation time of the organism increases (12). Additionally, although reciprocal transplants will detect signs of local adaptation, they are not necessarily suited to identifying the environmental drivers of that local adaptation (14). This is because *in situ* reciprocal transplants necessarily encompass all the environmental variables that differ between the transplant locations. Lab-based common garden approaches may, in principle, be more suited to identifying environmental drivers (because the environment may be under a degree of control), but in practice it often remains impossible to identify the environmental drivers of trait variation seen in the wild. Thus, the best experimental tools we have for studying local adaptation are demanding in terms of time and cost, and are unsuitable for assigning environmental drivers (such as climate variables) to adaptive variation. If we are looking for climate-driven local adaptation, this is a problem: we want to know which climate variable or variables are the main drivers of adaptation, and we urgently need this information for many species.

By definition, local adaptation has a genetic basis and is consequently weakened by gene flow (11, 15, 16). Demes with high levels of inward gene flow are therefore likely to be less optimally adapted, causing an observable mismatch between optimal and actual phenotypes. Some examples of this are birds dispersing and producing clutch sizes that are not optimised for the habitat quality in which they are now

115 nesting (17), larval salamander colouration not matching streambed colouration due to
116 high levels of gene flow from nearby but predator-free streams (18), and stick insects
117 in smaller habitat patches having non-cryptic colouration when the surrounding
118 patches are larger and environmentally dissimilar (19). These observations of
119 "migrant load" suggest an alternative technique for identifying and assessing local
120 adaptation. First, we look across populations for correlations between the environment
121 (e.g., mean annual temperature) and traits (e.g., morphology, physiology). By
122 themselves, these correlations are not sufficient evidence of local adaptation — they
123 could also be caused by phenotypic plasticity. Second, knowing that local adaptation
124 is hindered by gene flow, we can look at whether gene flow diminishes the
125 environmental effect. In cases where data on gene flow are absent (which is often the
126 case), habitat connectivity can be used as a substitute for gene flow. Environment–
127 trait correlations that are strong, but which are also weakened by connectivity, are
128 indicative of environment–trait correlations that have arisen through local adaptation.
129
130 If we now collect data on a large number of environment–trait correlations, and their
131 interaction with connectivity, we can imagine several possible patterns emerging.
132 These possibilities are depicted in Figure 1. Each panel represents a possible
133 relationship between environment–trait correlations (environmental coefficients on
134 the x-axis) and the interaction between environment and connectivity (y-axis). Panel
135 A shows a set of environment–trait relationships that are strong, but that are not
136 influenced by connectivity (i.e., no environment–connectivity interaction). This
137 pattern is indicative of a system in which environment–trait correlations are
138 predominantly driven by plastic responses of traits to their environment (i.e., traits
139 always match the local environment, regardless of the level of inward gene flow).

Plastic responses are still of interest, and many species are likely to show such plasticity as the climate changes (20). Panel B shows a system in which environment–trait relationships are eroded by connectivity: increased connectivity diminishes the correlation between the environment and the trait. In this situation, the interaction between the environmental variable and connectivity is negative when the environmental coefficient is positive (i.e., greater connectivity causes the environmental coefficient to decrease towards zero; bottom-right quadrant), and positive when the environmental coefficient is negative (i.e., greater connectivity causes the environmental coefficient to increase towards zero; top-left quadrant). This is the pattern we would expect if there is a genetic basis to the environment–trait correlation, i.e., local adaptation. Panel C shows the situation where the effect of the environment tends to be enhanced by connectivity. This pattern might arise in organisms that are highly mobile and can actively move to their ideal environment, thus avoiding the selective pressures that would lead to local adaptation.

Understanding how species respond to specific aspects of their environment is vital if we are to have any hope of halting the current rapid loss of biodiversity. Climate change is undoubtedly one of the biggest threats to global biodiversity (21, 22), and conservation biologists are looking to a variety of techniques to assess and help mitigate the impacts of climate change on vulnerable species (23-25). One technique that is likely to see increasing use is targeted, or assisted gene flow [TGF; for review, see (23, 26)]. This technique involves the spatial redistribution of long-standing adaptations, and acts to increase genetic diversity in recipient populations, thereby bolstering capacity for evolutionary adaptation (10, 23, 25, 26). When applying TGF to help species adapt to climate change, we need to find an existing location that

matches the future climate at our recipient site, and then translocate animals from that source location. It is a simple idea, but climate is multidimensional and species will not be adapting equally to each climate axis: is a difference of 0.5°C in mean temperature more important than a difference of 100mm in annual rainfall? The answer depends upon which axes have the strongest influence on fitness.

Here we explore the idea of using connectivity to infer local adaptation. To do this we develop a case study of a lizard species from northern Australia. We use this system to examine the relationship, across sites, between traits and climatic variables. We assess how habitat connectivity affects these relationships and use the interaction between the environmental variable and connectivity to rank environment–trait combinations. In doing so, we reveal a set of environment–trait relationships dominated by local adaptation.

Methods

Study species and site selection

The Rainforest Sunskink (*Lampropholis coggeri*) is a small (snout–vent length up to 45 mm), diurnal scincid lizard restricted to the rainforests of the Wet Tropics region of northeastern Australia (27). The rainforests of this region cover a wide range of environmental conditions, spanning significant elevation (0–1600 m ASL), precipitation (annual mean precipitation of 1432–8934 mm, not including input from cloud stripping), and temperature (annual mean temperature of 16.3–25.8˚C) gradients. This heliothermic skink is active year-round, often seen basking in patches

189 of sunlight on the rainforest floor. Lizards were captured by hand from sites that were
190 selected to maximize the environmental heterogeneity sampled (Fig. 2).
191
192 Morphological measurements were obtained from 532 skinks from 32 sites.
193 Physiological measurements were obtained from a smaller subset of these lizards: 259
194 skinks from 12 sites. Between 8–20 skinks were caught at each site on each collecting
195 trip. Following capture, skinks were transported to James Cook University (JCU) in
196 Townsville for trait measurement. All procedures involving lizards were approved by
197 the JCU animal ethics committee (projects A1976 and A1726).
198
199 Physiological trials
200 Physiological trials commenced within seven days of skinks being collected from the
201 field; skinks being used only for morphology were measured and released back at
202 their point of capture within seven days. The following measures were taken from
203 each skink (n = 259) during laboratory trials: critical thermal minimum (CTmin),
204 critical thermal maximum (CTmax), thermal-performance breadth for sprinting
205 (breadth80), maximum sprint speed (Rmax), temperature at which sprint speed is
206 optimized (Topt), active body temperature as measured in a thermal gradient
207 (Tactive), and desiccation rate (des) (see Table S1 for further details). Details of trait
208 measurement procedures are detailed elsewhere (see 28, 29).
209

Morphological measurements

The following measurements were taken from each skink (n = 532) using digital calipers: head width (HeadW); head length (HeadL); interlimb length (ILimbL); hindlimb length (HindLL). Left and right measurements were averaged to obtain one measurement for that trait. We also recorded snout–vent length (SVL), total length, and mass (see Table S1 for further details). All measurements were taken by one person (SLM) to minimize observer bias. All morphological variables were log-transformed prior to regression analyses.

Climatic variables, and connectivity

As our study aimed to assess adaptation to local climate, various temperature and precipitation variables were extracted for each site (see Table S2 for details). We considered both means and extremes. It is important to consider climatic extremes, because temperature extremes may be increasing faster than mean temperatures (30), and many species are likely to be particularly vulnerable to these extremes (31). Many environmental variables are highly correlated (28), so only the less-derived variables were used in analyses, specifically: annual mean precipitation (AMP); seasonality of precipitation (Pcov); precipitation of the driest quarter (Pdry); annual mean temperature (AMT); coefficient of variation of temperature (Tcov); average minimum daily temperature (Tmin); average maximum daily temperature (Tmax); average variance of daily maximum temperature (TmaxVar); and average variance of daily Tmin (TminVar).

Our connectivity index was designed to capture the flux of individuals through a location and is detailed in the Supplementary Material. Briefly, it is a measure of habitat suitability for our focal skink species, averaged over space using a species-specific estimate of dispersal potential. As our species is an obligate rainforest-dweller, grid cells in the landscape that are rainforest and that are surrounded by rainforest have high connectivity indices, while grid cells of rainforest surrounded by non-rainforest matrix have low indices. See Table S2 for further details on all variables, and Figure S1 for correlations between all variables.

Analysis

Our analysis aimed to assess: 1) the relationship, across sites, between each trait and each environmental variable; and 2) how connectivity affected each of these relationships (i.e., the interaction between connectivity and environment). To allow comparison of coefficients across variables, and to make interaction effect-sizes meaningful, all trait and environmental variables were standardized so they had a mean of 0 and a standard deviation of 1. Linear models were fitted for each pair of environment–trait variables, with all models including the effect of lizard body size and sex, as well as the interaction between environment and connectivity:

$$\text{trait}_i = A + B_{svl}\times\text{SVL}_i + B_{sex}\times\text{Sex}_i + B_{env}\times\text{Env} + B_{conn}\times\text{Conn} + B_{int}\times\text{Env}\times\text{Conn} + error_i$$

Where:

trait_i = standardized trait value of interest for lizard *i*

A = intercept

B_{svl} = coefficient of SVL

SVL = lizard snout–vent length, to control for effect of body size

B_{sex} = coefficient of Sex

Sex = lizard sex (this species is sexually dimorphic in some morphological traits)

B_{env} = coefficient of environmental variable

Env = environmental variable (e.g., annual mean temperature) at the lizard's site

B_{conn} = coefficient of connectivity

Conn = connectivity index at the lizard's site

B_{int} = coefficient of interaction between Env and Conn

$error_i$ = deviation between expected value and trait value of lizard *i*

A score for ranking the strength of local adaptation was then calculated as:

$$L = -B_{env}\, B_{int}$$

If the signs of the two coefficients (B_{env} and B_{int}) are opposite (which indicates an environmental effect being eroded by high connectivity, i.e., evidence for local adaptation), L will be positive. If the signs are the same (which indicates an environmental effect being enhanced by high connectivity, a situation not consistent with local adaptation), L will be negative. Thus, higher numbers on this scale equate to stronger evidence for local adaptation in that environment–trait pair. This score can, in theory, range from $-\infty$ to $+\infty$. Once many environment–trait combinations have been assessed, the coefficients for all pairs can be plotted (see Fig. 1). As described in the Introduction, in a system dominated by local adaptation, we expect to see a negative relationship between B_{env} and B_{int} (Fig. 1B). All analyses were conducted in R v3.2 (32).

Results

There was substantial variation in the effect of environment (B_{env}) and its interaction with connectivity (B_{int}) across climate and trait variables, with B_{env} ranging from -1.64 to 1.37, and B_{int} ranging from -0.89 to 0.74 (Fig. 3). Despite this variation, a clear pattern is evident, with most points in Figure 3 appearing in the top-left or bottom-right quadrants: the quadrants in which the two coefficients have opposing signs, and where we would expect points to fall if environment–trait relationships are due to local adaptation. Across these environment–trait combinations there is a distinct negative linear trend (slope= -0.36, $p < 0.001$). It is especially noteworthy that the environment–trait pairs with the largest coefficients (i.e., those points furthest away from the origin) are in the two quadrants indicative of local adaptation.

Overall, physiological traits showed substantially stronger environmental effects (i.e., larger values of B_{env}) than did morphological traits, with the largest environmental effects being exhibited by CTmin (AMP: -1.64; Tmax: 1.31; Pdry: 1.28) and CTmax (Pdry: 1.37). Physiological traits also showed stronger interactions between environmental effects and connectivity, again with CTmin and CTmax showing the largest interactions. These trends are apparent when we examine our index of local adaptation, L. Figure 4 shows a heatmap of all environment–trait pairs, ranked via reciprocal averaging according to the strength of their local adaptation index. The environment–trait pairs that show the strongest signature of local adaptation appear at the top-left in red. There is a rough divide, with most of the physiological traits on the left and most of the morphological traits on the right. The exceptions are the physiological traits Topt and Rmax, which appear at the far right of the figure.

The two environmental variables that produced the strongest effects (topmost rows in Fig 4) were both precipitation related: annual mean precipitation (AMP) and precipitation of the driest quarter (Pdry). In our system, AMP and Pdry are both highly correlated with connectivity (see Fig. S1). This is expected, because our connectivity index is largely a measure of where rainforest is, and the distribution of rainforest in our study region is driven to a large degree by rainfall.

Discussion

Understanding environment–trait correlations will help us plan management strategies, such as targeted gene flow (TGF), that can mitigate the impact of climate change on vulnerable species. Numerous studies have looked for (and found)

environment–trait correlations (e.g., 18, 19, 33, 34-36), but the interpretation of these associations is plagued with uncertainty: are they associations due to local adaptation, or plasticity? By acknowledging that gene flow undermines adaptation, we can incorporate connectivity (a proxy for the flux of genes) into our analysis, and in doing so, separate correlations due to local adaptation from those due to plasticity.

Local adaptation

In the environment–trait combinations we assessed, physiological traits typically showed a substantially stronger effect of environment than did morphological traits, with the largest environmental effects shown in CTmax and CTmin (Figs. 3 & 4). Physiological traits also generally showed stronger environment–connectivity interactions, again with CTmin and CTmax showing the largest interactions. Overall, physiological traits generally showed stronger evidence of local adaptation than did morphological traits. This result is intuitive: we would expect an ectotherm's physiological traits to be under strong selection from climate (37-39), but the fitness link between morphology and climate is much less clear. Had we also included some environmental variables that had a clearer bearing on morphology, we might have detected stronger environment–trait relationships for morphology. For example, skinks that occur in rockier habitats show various morphological adaptations to that environment (40). Including a measure of rockiness in our set of environmental variables, for example, might have allowed us to detect environmental correlations with limb length.

Of the environmental variables used, our analysis suggests that precipitation is a very strong driver of local adaptation, even in thermal traits that might not seem obviously

related to precipitation (e.g., CTmin, CTmax). Although this may seem a surprising result, precipitation has been shown to directly affect growth rate, body temperature, activity patterns, and thermoregulatory opportunities in lizards (38, 41-45). Wetter areas also have higher thermal inertia (and so lower cyclical thermal fluctuations (46)), and changed environmental variance in temperature potentially has a strong influence on thermal limits (47). Additionally, Bonebrake and Mastrandrea (48) found that changes in precipitation can significantly affect modeled fitness and performance curves. Finally, comparative analyses also suggest that precipitation can influence thermal traits in many species (38). Thus, although the mechanisms linking precipitation to thermal limits are diffuse and poorly resolved, they do exist, and our analyses suggest that precipitation is a strong driver of local adaptation at thermal physiological traits.

Our analysis also suggests that temperature is an important driver of local adaptation in this system, but that extremes of temperature (encapsulated in minimum and maximum temperatures) are at least as strongly associated with local adaptation as is mean temperature. Again, this result is intuitive (natural selection from climate is likely stronger during extreme events than during normal daily temperatures) and agrees with results of empirical studies (38). Finally, the environmental variables with the weakest signals of local adaptation are Tcov (temperature seasonality), TminVar, and TmaxVar (variance of minimum and maximum daily temperatures, respectively). These variables represent predictable environmental variation occurring within an individual's lifespan and so are variables to which we might expect individuals to develop plastic responses, rather than adaptive responses (49-51).

370 System-wide signal of local adaptation

371 The clear negative linear trend displayed in Fig. 3 is precisely what we would expect
372 in a set of environment–trait combinations dominated by local adaptation. Migrant
373 load (the negative effect of the immigration of less-locally adapted individuals) scales
374 positively with immigration as well as with the strength of selection [see equation 5 in
375 Polechová, Barton and Marion (52)]. The reason for this is that, when the strength of
376 selection is moderately high, the environment will have a large effect on relevant
377 traits, and therefore any immigrants coming from differing environments will be
378 particularly maladapted and will therefore have a large and negative impact on the
379 local phenotype. Thus, we expect environment–trait combinations with strong local
380 adaptation to show strong effects of connectivity on the environment–trait correlation
381 (52).

382

383 We used long-term climatic averages and found strong evidence that local adaptation
384 dominates over plasticity in our system. If we had included different environmental
385 variables, such as the conditions the lizards had recently encountered, signals of
386 plasticity may have been more apparent. Clearly environmental variables that are
387 similar across generations should lead to local adaptation, while environmental
388 variables that fluctuate within generations should have a strong influence on
389 phenotypic plasticity

390

391 Phenotypic plasticity

392 The importance of accounting for phenotypic plasticity is exemplified in our dataset
393 by the relatively strong effect of precipitation of the driest quarter (Pdry) on the
394 temperature at which maximum sprint speed is achieved (Topt) and on maximum

395 sprint speed (Rmax) itself. On their own, these strong correlations might traditionally
396 be considered evidence for local adaptation. Our analysis, however, suggests that the
397 environmental effect is largely unaffected by connectivity, implying that variation in
398 these traits is due to plasticity. Other work (28) has shown little temporal variation in
399 Topt (within generations) despite clear geographic variation and this, together with
400 our results, suggests that this trait undergoes developmental plasticity, but is fixed in
401 adult lizards. In principle, this non-effect of connectivity could also arise due to
402 selection that is so strong that it maintains local adaptation despite high levels of gene
403 flow [i.e., immigrants are selected against so strongly that they do not contribute to
404 the effective population (11)]. The environment–trait relationships for Topt and Rmax
405 are, however, weaker than those for some other traits (e.g., CTmax and CTmin) that
406 show clear effects of connectivity, so extremely strong selection seems an unlikely
407 explanation for the pattern we see here.
408
409 Assumptions and limitations
410 Our analysis requires an index of population connectivity across the landscape,
411 something that can be calculated relatively easily for many species by using broad
412 scale habitat mapping datasets [e.g., vegetation mapping from DERM (53)]. Where
413 possible, these measures of connectivity should be calculated at a scale relevant to the
414 scale of dispersal of the species in question [as was ours, using dispersal rate data for
415 *Lampropholis coggeri* from Singhal and Moritz (54)]. For highly mobile species, such
416 as plants or insects that have wind-assisted dispersal and for which calculating
417 connectivity between populations may be difficult, it is possible our approach will not
418 work. But for many species of animals with relatively low vagility (i.e., the species
419 for which TGF is most needed), our approach should be generally applicable.

Our approach implicitly assumes that traits have a linear response to the environment (at least at the environmental scale across which we are looking). In most instances, this will be a reasonable assumption: it seems unlikely, for example, that a trait such as desiccation resistance would be high in dry environments, low in moderately wet environments, and then high again in very wet environments. The reason our assumption of linear environment–trait relationships bears mentioning is that a limitation of our technique arises when the connectivity index is strongly correlated with one or more of the other environmental variables being used. In our system, for example, AMP and Pdry are correlated with connectivity (Fig. S1). Where the environment–connectivity correlation is very strong, the interaction term in our model (Conn×Env) could be interpreted as a quadratic term for environment (i.e., Env^2). In these cases, it is possible that a strong connectivity interaction is, in fact, pointing to a non-linear environment–trait relationship. Thus, for environmental variables that correlate with connectivity (and there will always be some), careful consideration needs to be given to the possibility of a quadratic fitness function between environment and trait. In our case, it remains possible, for example, that the strong influence of precipitation on local adaptation in our system is spurious, and instead reflects non-linear relationships between optimal trait values and precipitation. We can, however, think of no obvious reason why thermal limits should respond quadratically to precipitation, nor why desiccation rates and other physiological traits should also do so. Thus we are inclined to accept the importance of this environmental variable in driving local adaptation in our system.

Finally, our approach, by examining one environment–trait combination at a time, may potentially miss relationships that only appear in multivariate analyses. For example, if two environmental variables are negatively correlated but both have a positive effect on a trait, it is possible that these countergradients can obscure the univariate relationship. Similar problems are encountered when examining response to selection over time (55), and with our approach may lead us to underestimate the number of important environmental drivers of local adaptation. To minimize this effect, care should be taken in future work to sample environmental spaces in such a way as to minimize correlations between environmental variables. Such an aim can be achieved by, for example, strategically exploiting latitudinal and altitudinal gradients.

Conclusion

There is increasing urgency to identify populations that will act as suitable sources for targeted gene flow efforts in the face of climate change. To identify these populations, we need to know which traits influence sensitivity to climate and are locally adapted. Traditional approaches to unearthing local adaptation (reciprocal transplants and common garden experiments) are time consuming, and often cannot attribute adaptation to any particular environmental driver. Local adaptation is, however, undermined by gene flow, and we should be able to use this fact to sort patterns of local adaptation from patterns with other causes. Here we have demonstrated this approach: using connectivity as a proxy for gene flow, and looking for its effect on environment–trait correlations. Our analysis, using a species of lizard from Australia's Wet Tropics rainforest, suggests the approach has merit: the results we achieve are coherent and suggest local adaptation is the overwhelming signal in the set of environment-trait correlations tested. As well as confirming a strong role for local

adaptation, we have effectively ranked environmental drivers of local adaptation, finding evidence that precipitation and temperature are important environmental variables with regard to local adaptation. Our analysis also suggests that some traits exhibit strong plastic responses to the environment, particularly in response to precipitation of the driest quarter and the seasonality of temperature and precipitation. These specific results will likely apply to other species that are phylogenetically or ecologically similar to our focal species, but the method has the potential to apply much more broadly. Given the potential of this method to provide evidence of local adaptation, and rapid ranking of the climatic drivers of local adaptation, assessment of the method in a broader array of systems is warranted.

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Figure Captions

Figure 1. Graphs showing the concepts illustrated by plotting a set of environment–trait coefficients (x-axis) and the corresponding environment–connectivity interaction coefficients (y-axis). A) Phenotypic plasticity is suggested when environment–trait relationships are strong, but are not influenced by connectivity. B) Local adaptation is suggested when increasing connectivity diminishes the correlation between the environment and the trait. C) The effect of the environment is enhanced by connectivity. This latter pattern might arise in organisms that are highly mobile and can actively move to their ideal environment, thus avoiding the selective pressures that would lead to local adaptation.

Figure 2. Map of the southern Australian Wet Tropics bioregion, showing the distribution of rainforest and the sampling locations.

Figure 3. Scatterplot showing the results of 99 linear models run to assess the relationship between each pair of environment–trait variables and the environment–connectivity interaction. Environment–trait coefficients are on the x-axis, and environment–connectivity interaction coefficients are on the y-axis. Local adaptation is suggested in environment–trait pairs that show a strong environmental effect that is eroded by increasing connectivity.

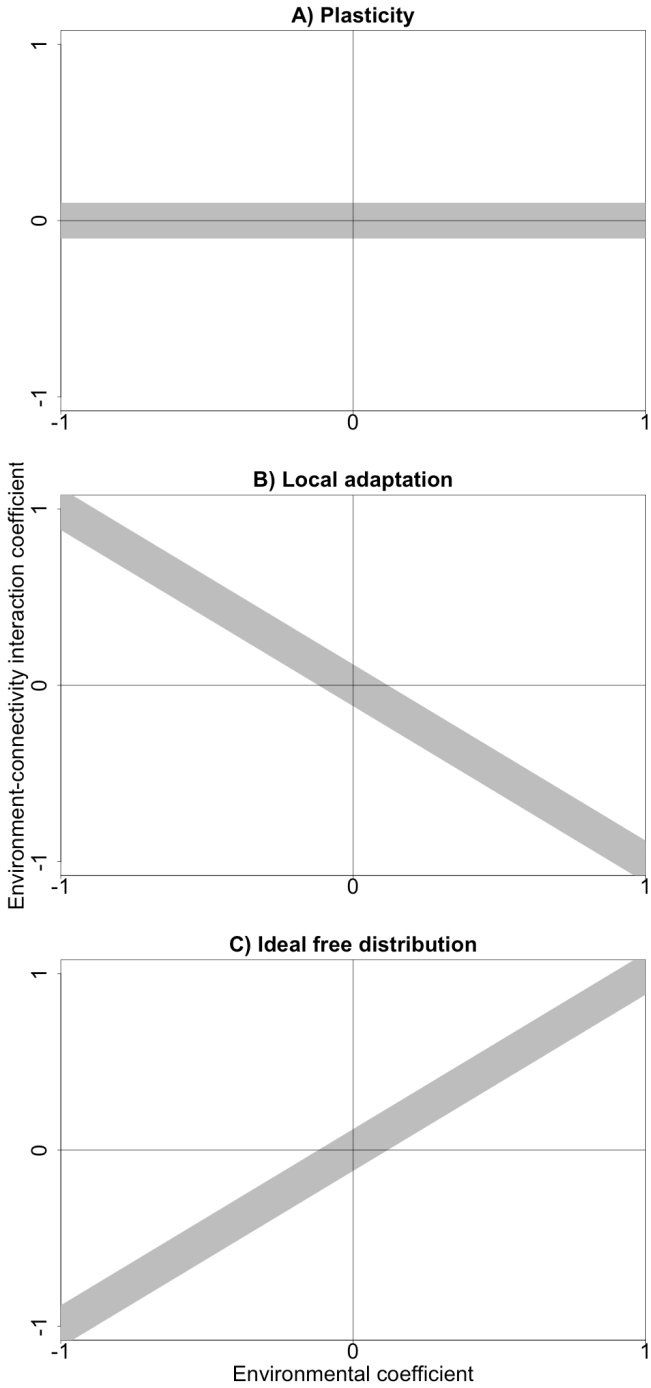
Figure 4. Heatmap showing the relative rankings of climate variables (rows) and morphological and physiological traits (columns). The matrix has been sorted (by reciprocal averaging) and coloured according to the strength of local adaptation, with higher values coloured red and being sorted to the top/left. See Tables S1 and S2 for explanations of the trait and environmental variables used.

L = local adaptation index: $-B_{env}\ B_{int}$

B_{env} = coefficient of the environmental variable.

B_{int} = coefficient of the interaction between the environment and connectivity terms.

674 **Figures**



675

676 **Figure 1**

677

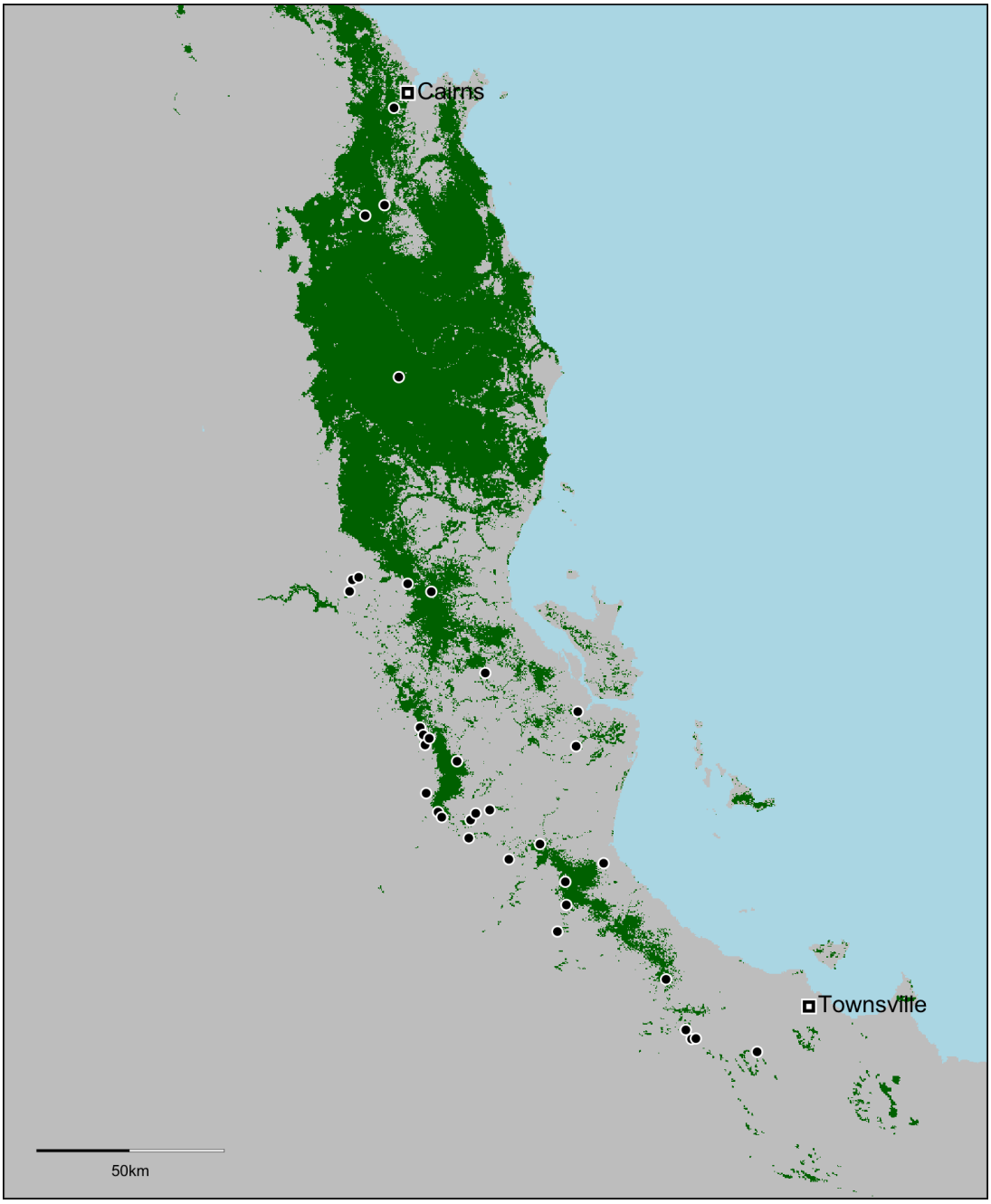


Figure 2

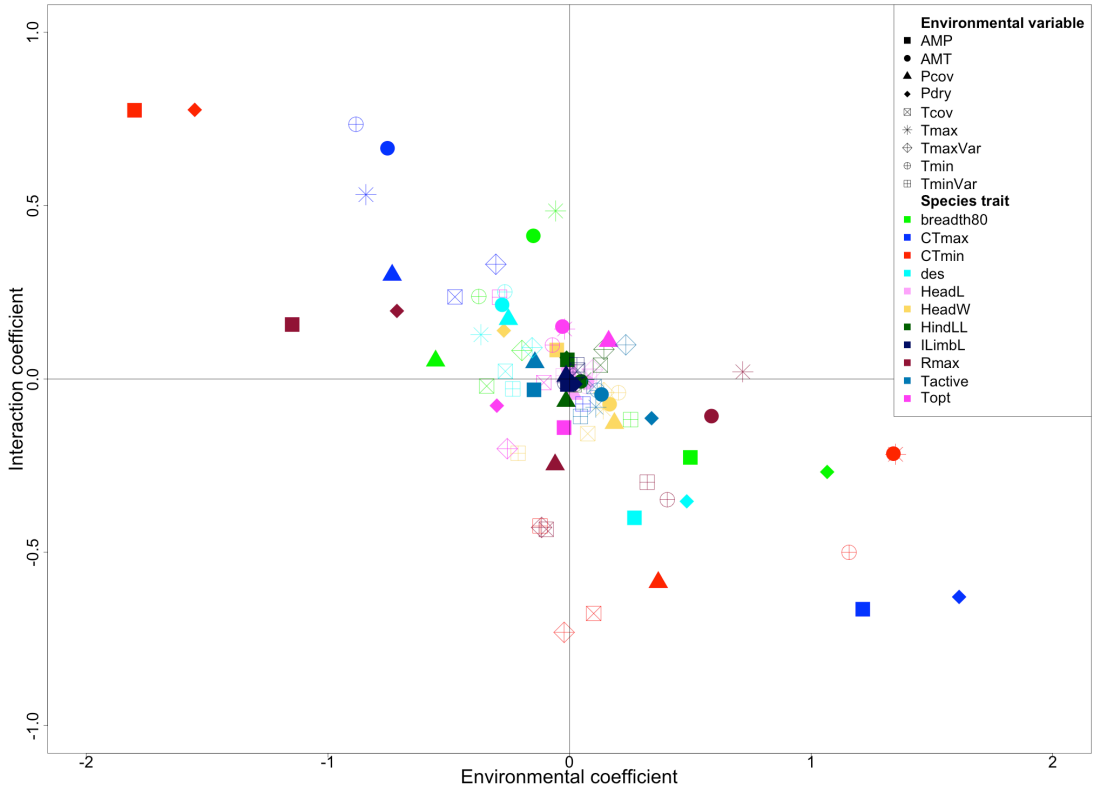

Environmental variable
AMP
AMT
Pcov
Pdry
Tcov
Tmax
TmaxVar
Tmin
TminVar
Species trait
breadth80
CTmax
CTmin
des
HeadL
HeadW
HindLL
ILimbL
Rmax
Tactive
Topt
Interaction coefficient
Environmental coefficient
1.0
0.5
0.0
-0.5
-1.0
-2
-1
0
1
2

Figure 3

	CTmin	CTmax	breadth80	Rmax	des	HeadW	Tactive	HindLL	HeadL	ILimbL	Topt
AMP	L = 0.7751	L = -0.6644	L = -0.2265	L = 0.1570	L = -0.4007	L = 0.0835	L = -0.0315	L = 0.0551	L = 0.0219	L = -0.0159	L = -0.1404
Pdry	L = 0.7763	L = -0.6289	L = -0.2683	L = 0.1961	L = -0.3532	L = 0.1395	L = -0.1134	L = 0.0613	L = 0.0279	L = -0.0150	L = -0.0771
Tmin	L = -0.5004	L = 0.7345	L = 0.2380	L = -0.3484	L = 0.2510	L = -0.0399	L = -0.0329	L = -0.0157	L = -0.0219	L = -0.0116	L = 0.0977
AMT	L = -0.2156	L = 0.6655	L = 0.4128	L = -0.1072	L = 0.2139	L = -0.0730	L = -0.0447	L = -0.0071	L = -0.0099	L = -0.0043	L = 0.1511
Tmax	L = -0.2173	L = 0.5316	L = 0.4846	L = 0.0206	L = 0.1275	L = -0.0864	L = -0.0813	L = -0.0020	L = -0.0041	L = 0.0002	L = 0.1438
Pcov	L = -0.5868	L = 0.2996	L = 0.0522	L = -0.2473	L = 0.1719	L = -0.1279	L = 0.0474	L = -0.0642	L = -0.0440	L = 0.0082	L = 0.1089
Tcov	L = -0.6766	L = 0.2366	L = -0.0206	L = -0.4338	L = 0.0219	L = -0.1579	L = -0.0219	L = 0.0397	L = 0.0083	L = 0.0253	L = -0.0104
TmaxVar	L = -0.7312	L = 0.3308	L = 0.0820	L = -0.4284	L = 0.0898	L = -0.0394	L = 0.0984	L = 0.0853	L = 0.0267	L = 0.0034	L = -0.2013
TminVar	L = -0.4241	L = -0.0721	L = -0.1174	L = -0.2979	L = -0.0289	L = -0.2144	L = -0.1083	L = -0.0172	L = 0.0095	L = 0.0409	L = 0.2357

Figure 4