

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19

Received Date:

Revised Date:

Accepted Date:

Article Type: Original Article

Corresponding author mail id :- [mgrundler@berkeley.edu](mailto:mgrundler@berkeley.edu)

Title: Is genomic diversity a useful proxy for census population size? Evidence from a species-rich community of desert lizards

Authors: Maggie R. Grundler<sup>1,2\*</sup>, Sonal Singhal<sup>1,3</sup>, Mark A. Cowan<sup>4</sup>, Daniel L. Rabosky<sup>1</sup>

<sup>1</sup>Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109

<sup>2</sup>Department of Environmental Science, Policy, & Management, University of California, Berkeley, Berkeley, CA 94720

<sup>3</sup>Department of Biology, CSU Dominguez Hills, Carson, CA 90747

<sup>4</sup>Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia 6151

\* Corresponding Author

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/MEC.15042](https://doi.org/10.1111/MEC.15042)

This article is protected by copyright. All rights reserved

20 ABSTRACT

21 Species abundance data are critical for testing ecological theory, but obtaining accurate empirical  
22 estimates for many taxa is challenging. Proxies for species abundance can help researchers  
23 circumvent time and cost constraints that are prohibitive for long-term sampling. Under simple  
24 demographic models, genetic diversity is expected to correlate with census size, such that  
25 genome-wide heterozygosity may provide a surrogate measure of species abundance. We tested  
26 whether nucleotide diversity is correlated with long-term estimates of abundance, occupancy,  
27 and degree of ecological specialization in a diverse lizard community from arid Australia. Using  
28 targeted sequence capture, we obtained estimates of genomic diversity from 30 species of  
29 lizards, recovering an average of 5,066 loci covering 3.6 Mb of DNA sequence per individual.  
30 We compared measures of individual heterozygosity to a metric of habitat specialization to ask  
31 whether ecological preference exerts a measurable effect on genetic diversity. We find that  
32 heterozygosity is significantly correlated with species abundance and occupancy, but not habitat  
33 specialization. Demonstrating the power of genomic sampling, the correlation between  
34 heterozygosity and abundance/occupancy emerged from considering just one or two individuals  
35 per species. However, genetic diversity does no better at predicting abundance than a single day  
36 of traditional sampling in this community. We conclude that genetic diversity is a useful proxy  
37 for regional-scale species abundance and occupancy, but a large amount of unexplained variation  
38 in heterozygosity suggests additional constraints or a failure of ecological sampling to adequately  
39 capture variation in true population size.

40 Keywords: heterozygosity, species abundance, Lewontin's paradox, target capture, squamates

41  
42 INTRODUCTION

43  
44 Species abundance distributions represent one of the most basic descriptions of a  
45 community, and are the foundation of many ecological theories and conservation management  
46 practices (He and Gaston 2000; McGill et al. 2007). Relative abundance is typically estimated  
47 through repeated community sampling efforts, with study durations that frequently span multiple  
48 years (Magurran et al. 2010; Meyer et al. 2010; Gotelli and Chao 2013; Pianka 2014). An

49 obvious difficulty is that such "brute-force" sampling requires considerable time and funding in  
50 order to produce reliable estimates (Pearce and Ferrier 2001; Yin and He 2014). Consequently,  
51 there has been widespread interest in developing statistical methods for estimating relative  
52 species abundance from imperfect survey data as well as from proxy variables, including point  
53 occurrences, spatial distributions, and environmental suitability (He and Gaston 2000;  
54 Jeremy VanDerWal et al. 2009; Yin and He 2014). Although these methods perform well at  
55 small spatial scales, predicting regional abundance remains challenging, in part because of the  
56 paucity of data available to validate model-predicted abundances (Pearce and Ferrier 2001; Yin  
57 and He 2014).

58 Neutral theory predicts that genetic diversity should correlate with population census size  
59 (Tallmon et al. 2010; Wright 1931; Leffler et al. 2012), and intraspecific genetic variation is thus  
60 an attractive proxy for species abundance in natural populations. Genetic material is both easy  
61 and inexpensive to sample (Schwartz et al. 2007), and recent advances in sequencing technology  
62 and bioinformatics allow researchers to harvest information from across the genome at low cost.  
63 Furthermore, reliable estimates of both genetic diversity and past population size have been  
64 recovered from samples sizes as small as a single individual (Li and Durbin 2011; Nazareno et  
65 al. 2017). However, historical signals of demographic processes can weaken the relationship  
66 between census and effective population size, and thus the relationship between abundance and  
67 heterozygosity (Frankham 1995). For example, range expansions or population bottlenecks can  
68 lead to reduced genetic diversity in marginal or founder populations, and consequent decoupling  
69 from contemporary census population size (Excoffier and Ray 2008; Charlesworth 2009; Banks  
70 et al. 2013; Dalongeville et al. 2016).

71 Previous studies have found positive relationships between heterozygosity and proxies  
72 for species abundance, including population size estimated from calculations of density and  
73 acreage (Patton and Yang 1977), extrapolations calculated from active social groups (Stangel et  
74 al. 1992), categorical estimates ("large", "small") of population size (Godt et al. 1996; Hague and  
75 Routman 2016), and museum occurrence records (Singhal et al. 2017b). Studies that more  
76 directly compare intraspecific genetic diversity and abundance have reported positive  
77 associations, but these studies have generally focused on single species or paired species  
78 comparisons (Lozier 2014; Sun 1996; Ortego et al. 2008; Devillard et al. 2011), or on many  
79 species sampled at a broad geographic scale (Bazin et al. 2006; Leimu et al. 2006; McCusker and

80 Bentzen 2010; Pinsky and Palumbi 2014). Few studies have directly assessed the relationship  
81 between abundance and genetic diversity within species-rich communities of potentially  
82 interacting species, despite the importance of such communities for biodiversity monitoring and  
83 studies of eco-evolutionary dynamics.

84 In addition to these rather practical motivations, the ecological analysis of genetic  
85 variation may help us to understand why the range of genetic diversity among species is orders  
86 of magnitude smaller than that of census population size. This observation represents a long-  
87 standing but unresolved puzzle for evolutionary biology known as “Lewontin’s paradox”  
88 (Lewontin 1972; Leffler et al. 2012). Addressing this knowledge gap may be especially critical  
89 for conservation efforts, which would benefit from a comprehensive understanding of which  
90 factors constrain genetic diversity and influence effective population size in wild populations  
91 (Palstra and Ruzzante 2008; Leffler et al. 2012).

92 Foundational studies based on results from a small number of loci, including  
93 microsatellites characterized by high variability in mutation rate, found few discernible links  
94 between genetic polymorphism and ecological traits (Ellegren and Galtier 2016). Genome-wide  
95 data increase our power to recover associations between genetic diversity, ecological correlates,  
96 and evolutionary processes acting over shorter time periods (Faircloth et al. 2012; Harvey et al.  
97 2017). Recent studies have found strong relationships between ecological traits and genetic  
98 diversity at broad phylogenetic scales (e.g. across phyla; (Romiguier et al. 2014)); whether such  
99 patterns are also exhibited by more closely-related species with similar life history traits remains  
100 equivocal (Romiguier et al. 2014; Ellegren and Galtier 2016; Singhal et al. 2017b). Additionally,  
101 there is some evidence that microhabitat preference can limit dispersal and reduce within-  
102 population genetic diversity (Pianka 1986; Brouat et al. 2003; Brouat et al. 2004; Rabosky et al.  
103 2011; Pianka 2014; Dalongeville et al. 2016; Khimoun et al. 2016), but studies combining  
104 genome-wide diversity estimates with ecological traits at the community level are rare.

105 In this study, we test whether genome-wide estimates of heterozygosity are correlated  
106 with species abundance, landscape-level occupancy, and habitat specialization. We focus on a  
107 species-rich community of lizards from the western Australian arid zone that has been subject to  
108 multi-year demographic study and is characterized by variation in abundance and other  
109 ecological traits (Pianka 1986; Rabosky et al. 2011; Pianka 2014; Grundler et al. 2017). Despite  
110 ecological variation among clades, species in this community are generally similar in major life

111 history characteristics (Mesquita et al. 2016) and share a common geological and climatic  
112 history, potentially minimizing the confounding effects of variation in environment,  
113 demographic history, and phylogeny.

114 We also explore relationships with additional ecological traits that may relate to  
115 abundance, including habitat preference and body size. Based on classic theory and previous  
116 work, we predict that (1) greater species abundance will correlate with greater levels of  
117 nucleotide diversity; and (2) that increasing habitat specialization will correlate with reduced  
118 levels of nucleotide diversity, due to reduced gene flow between populations restricted by narrow  
119 ecological preference. We construct a multipredictor model to assess the relative importance of  
120 each of these ecological traits in explaining variation in heterozygosity. This framework provides  
121 a means of better understanding what ecological processes influence genetic diversity in light of  
122 Lewontin's paradox.

123

## 124 METHODS

125

126

### 127 *Sample and Ecological Data Collection*

128

129 Tissue samples from 30 species of lizards were collected by Rabosky et al. (2011) as part  
130 of a long-term monitoring project at the former pastoral station of Lorna Glen in the western  
131 Australian arid zone. This area is now known by its traditional name Matuwa, and hereafter will  
132 be referred to by this name. The Matuwa region – and the spinifex desert of the western  
133 Australian arid zone more generally – harbors the most diverse lizard communities on Earth  
134 (Pianka 1972; Morton and James 1988; James and Shine 2000; Roll et al. 2017), with potentially  
135 more than 50 species co-occurring at single sites from spinifex sandplain habitats (Pianka 1986;  
136 Rabosky et al. 2011). Species from which genetic data were obtained included representatives of  
137 at least four Australian lizard radiations, including sphenomorphine and non-sphenomorphine  
138 skinks, agamids, and geckos. Ecological data including long-term cumulative measures of  
139 species abundance, species habitat preference, and body size were collected as part of the same  
140 study. The data presented here include genetic and ecological data for an additional 10 species  
141 that were not included in Rabosky et al. (2011). Briefly, the study entailed multi-year pitfall

142 trapping of lizard communities at 24 sites at Matuwa, with sites selected to encompass the  
143 majority of habitats in the study region. Each site comprised two lines of six 20-L buckets buried  
144 in the substrate and connected by a continuous barrier of drift fencing. Sites were separated by  
145 approximately 3-10 km, and sampled for 21-28 days per year between 2002 and 2008. During  
146 each sampling period, traps on all sites were kept open for the same number of days, ensuring  
147 that sampling was standardized across the landscape. Further details on study design are  
148 available in Rabosky et al. (2007; 2011).

149 Abundance for each species was calculated as the sum of each annual survey total across  
150 sites. While even the most rigorous sampling methods cannot capture true population size across  
151 a region, the consistent effort applied to the Matuwa lizard community represents one of the most  
152 direct assessments of abundance feasible. Pitfall traps combined with drift fencing are an  
153 effective method for capturing arid Australian lizards (Morton et al. 1988). They are superior to  
154 alternative methods tested in this region (Cowan et al. 2017), and demonstrate low capture bias  
155 for the small-bodied taxa of this study, based on visual surveys by the authors.

156 To approximate habitat preference, fourteen habitat variables were measured for each  
157 pitfall trap included in the survey, accounting for variation in nearby vegetation type, substrate  
158 type, soil compaction and shear strength, woody debris, and distance to and diameter of nearest  
159 sheltering vegetation. Each individual lizard was associated with the habitat variables of the trap  
160 in which it was captured. Habitat variables were log-transformed and z-score standardized  
161 following methods reported by Rabosky et al. (2011). For each species composed of  $n$   
162 individuals, we calculated the Euclidean distance between habitat variables for all pairwise  
163 comparisons of individuals, resulting in an  $[n \times n]$  distance matrix. A simple index of habitat  
164 specialization was computed by taking the average of the distance matrix, excluding the  
165 diagonal. This final value provides an approximation of the average distance between two  
166 individuals in the habitat space occupied by a species, and is robust to variation in sample size  
167 between species. For example, individuals from a specialized species are expected to be  
168 associated with similar habitat variables (demonstrating adherence to a restricted set of  
169 environmental attributes) and therefore will generate a smaller average distance in this  
170 calculation, relative to generalist species.

171 We additionally compare genetic diversity to body size, a traditional proxy for species  
172 abundance whereby smaller species are expected to be more abundant (White et al. 2007). As

173 one of the most fundamental properties of an organism, body size is also thought to correlate  
174 with multiple aspects of trophic and other ecological and life history traits (Woodward et al.  
175 2005). We therefore include body size in the multipredictor model in the interest of  
176 understanding what factors contribute to variation in genetic diversity. The distributions of  
177 snout-vent length (SVL) within species were often multimodal, reflecting contamination by  
178 several distinct age cohorts of lizards (e.g., first-year juveniles; subadults) during our sampling  
179 periods (Rabosky et al. 2007). We thus used kernel density estimation (KDE) to estimate adult  
180 body size. This method is non-parametric, as the shape of the estimated density function is  
181 determined by the data without assuming an underlying distribution, and has been used for a  
182 variety of ecological applications (Manly 1996; Seaman and Powell 1996; Rabosky et al. 2011).  
183 Following Rabosky et al. (2007), we took the upper mode of the empirical probability density  
184 function for SVL for each species as representative of the "typical" adult body size.

#### 185 *Genomic Data Collection*

186 Methods for genomic data collection are identical to those described in greater detail by  
187 Singhal et al. (2017a). Using the high-salt DNA extraction method (Aljanabi and Martinez  
188 1997), we collected high molecular weight DNA from one individual per species for 19 of the 30  
189 species collected at Matuwa, and two individuals per species for 11 of the 30 species. Dual-  
190 barcoded libraries were produced for each sample by Arbor Biosciences (Ann Arbor, MI). Arbor  
191 Biosciences also designed probes at 2x tiling density across the 5,462 unique SqCL target loci  
192 identified by Singhal et al. (2017a), including anchored hybrid enrichment (AHE) loci,  
193 ultraconserved elements (UCEs) and traditional genes used in squamate phylogenetics (other  
194 loci). We refer to this set of loci as the SqCL marker set (Singhal et al. 2017a). Target capture  
195 reactions were performed on size-selected, amplified, and cleaned libraries following a modified  
196 MYbaits protocol described by Singhal et al. (2017a), and sequenced by Hudson Alpha on one  
197 100 paired-end run of a HiSeq 2500 v4.

#### 198 *Data Analysis*

199 To obtain estimates of nucleotide diversity, raw sequencing reads were analyzed  
200 following the bioinformatics pipeline provided for SqCL, available at  
201 <https://github.com/singhal/SqCL> along with explanatory documentation. Methods for the present  
202 study were modified to include error correction of cleaned reads using BLESS-EC2 before  
203 targets were matched to probes (Heo et al. 2016). To perform read error correction, an estimated

204 k-mer size was calculated using kmergenie with a default max length of 121, resulting in an  
205 optimal k-mer length of 31.

206 Within-population diversity was estimated by calculating the average pairwise difference  
207 ( $\pi$ ) across all loci for each individual (Tajima 1983; Begun et al. 2007). With greater than 5000  
208 loci, this is equivalent to estimating population diversity by sampling a few loci for many  
209 individuals (Willing et al. 2012; Harvey et al. 2017). For species that had two sampled  
210 individuals, we calculated  $\pi$  for each individual and then averaged the two measurements. All  
211 references to nucleotide diversity below refer to the average nucleotide diversity within a single  
212 individual, averaged across individuals within species for the 11 species where multiple  
213 individuals were sampled. Additionally, we calculated the Pearson correlation between estimates  
214 of nucleotide diversity for individuals from the same species and used ANOVA to estimate the  
215 variance explained within and between species. For each individual, nucleotide diversity was  
216 also calculated for each locus in order to produce bootstrapped estimates of genetic diversity  
217 with variation in the number of loci sampled.

218 To test the relationship between nucleotide diversity and ecological predictors, we  
219 performed a pairwise correlation analysis as well as phylogenetically-informed model selection,  
220 using the phylogeny from Tonini et al. (2016) (for this and all subsequent phylogenetic  
221 analyses), to estimate the importance of each predictor variable. We first computed the pairwise  
222 correlation between individual-level nucleotide diversity and the following ecological attributes  
223 for each species, using an expanded version of the Rabosky et al. (2011) dataset: species  
224 abundance, computed as the total number of individuals captured during the seven year survey  
225 period; and species occupancy, computed as the total number of sites where a species was  
226 detected. We note that our estimates of abundance are not based on an explicit capture-mark-  
227 recapture study, and we view the total number of individuals captured per species as a proxy for  
228 true total abundance (see Rabosky et al. 2011, for discussion). Because all sites were sampled for  
229 an identical number of days, we also note that all results reported below will be identical  
230 regardless of whether we analyze total abundance, mean annual abundance, or relative  
231 (fractional) abundance. We also included estimates of SVL and the proxy for species habitat  
232 specialization described above. We report  $p$ -values as the significance of each variable after  
233 accounting for phylogeny, calculated from phylogenetic linear models including only the  
234 predictor and genetic diversity, using Pagel's  $\lambda$  model for the covariance (Ho et al. 2018).



235 Because our primary hypothesis is that genetic diversity should be positively correlated with  
236 species abundance, we did not correct for multiple comparisons despite statistical tests including  
237 additional predictors. These analyses were conducted to facilitate interpretation of data  
238 concerning our primary hypothesis, and thus we do not believe multiple comparison correction to  
239 be appropriate for our study design.

240 To determine the relative importance of each predictor, we constructed phylogenetic  
241 generalized least squares (PGLS) models for the full model (4 predictors, not including  
242 interactions) and for each possible submodel, and we computed AIC weights using the full set of  
243 fitted models. Because ordinary least squares models assume unequal variance in error among  
244 dependent and independent variables, we confirmed homoscedasticity of the residuals of each  
245 submodel using a Breusch-Pagan test with a significance level of  $\alpha = 0.05$ . These tests verified  
246 the consistency of standard errors in all models; however, we note that error in the independent  
247 variables would bias slopes toward zero, thus making these models a conservative approach.

248 We then calculated the relative importance of each variable by summing the AIC weights  
249 of the models in which the variable appears and dividing this by the sum of the AIC weights of  
250 all models (Anderson and Burnham 2002; Kisel and Barraclough 2010). We constructed a final  
251 model including all variables with a relative importance greater than 0.6 to calculate coefficients  
252 and values of significance for the regression (Wagner et al. 2012).

253 Finally, to quantify the effectiveness of genetic diversity as a proxy for species  
254 abundance and facilitate comparisons with other methods, we computed the relative root mean  
255 squared error (rRMSE) of species abundance estimates predicted from heterozygosity, using the  
256 following equation from Yin and He (2014):

257 
$$rRMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n \left( \frac{x_i - o_i}{o_i} \right)^2}$$

258 where  $x_i$  is the predicted log abundance for species  $i$  based on a linear model with heterozygosity  
259 and empirical estimates of species log abundance;  $o_i$  is the observed abundance of species  $i$ ; and  
260  $n$  is the total number of species sampled. We additionally calculated Pearson's product-moment  
261 correlation and  $R^2$  values to quantify the significance of the correlation between observed and  
262 predicted abundance estimates, and compare these to alternative statistical models reported in  
263 Yin and He (2014) for predicting abundance.

264 As a second approach to evaluating the strength of genetic diversity as an abundance  
265 proxy, we performed a sliding-window resampling analysis to determine how many days of  
266 standardized community sampling are required to predict overall species abundance with the  
267 same correlation obtained from genetic diversity. In other words, how many consecutive days of  
268 sampling would have been required, on average, to recover a similar correlation between total  
269 abundance (across the full survey period) as that which we obtained from genetic data alone? We  
270 regenerated abundance and occupancy estimates beginning with a single day of sampling drawn  
271 from every unique date in the sampling period, increasing the window one day at a time from  
272 each starting point and averaging the results across dates within each window. For example, the  
273 mean correlation obtained for a window size of five days corresponds to the expected correlation  
274 between overall (multi-year) abundance and a much shorter sub-survey of just five sequential  
275 survey days.

276

## 277 RESULTS

278 We recovered an average of 4,728 UCEs, 309 AHEs, and 27 additional loci traditionally used in  
279 squamate phylogenetics for each individual, resulting in an average of 5,066 loci per individual  
280 with a total of 2,946 loci in common between all individuals. We recovered an average of 3.6 Mb  
281 for each individual, with an average of 3.16 Mb  $\geq$  10x coverage. Measuring diversity from  
282 thousands of loci provides more reliable estimates of individual-level heterozygosity among  
283 species, as demonstrated by wider variability in bootstrapped estimates of diversity from fewer  
284 loci (Fig. 1A). Eleven of 30 species were represented by two individuals, and nucleotide  
285 diversity between conspecifics was highly correlated (Pearson's  $r = 0.984$ ;  $p = 5.178 \times 10^{-8}$ ) (Fig.  
286 1B). Using ANOVA on this set of individuals, we estimate that intraspecific variation accounts  
287 for approximately 1.53% of the total variation in individual-level nucleotide diversity across our  
288 dataset. These results suggest that, with genome-wide sampling, even single individuals contain  
289 sufficient information to estimate "average" levels of within-population genetic variation.

290 Both log abundance and occupancy exhibited a positive and significant correlation with  
291 genetic diversity ( $r=0.43$ ,  $p = 0.02$ ;  $r=0.50$ ,  $p = 0.005$ , respectively; correlation coefficients are  
292 not phylogenetically corrected) (Fig. 2,3, Table S1). In line with Lewontin's paradox, our  
293 estimates of abundance varied across two orders of magnitude while genetic diversity varied  
294 across less than one. Abundance and occupancy are also highly correlated ( $r=0.70$ ,  $p = 1.5 \times 10^{-}$

295 <sup>5</sup>) (Fig. 3). There was no relationship between genetic diversity and log SVL ( $r = -0.10$ ,  $p =$   
296  $0.60$ ), but log SVL was negatively and significantly correlated with abundance ( $r = -0.49$ ,  $p =$   
297  $0.006$ ) (Fig. 3).

298 While there was a significant and positive relationship between occupancy and habitat  
299 specialization as approximated by the habitat distance metric ( $r = 0.52$ ,  $p = 0.003$ ), there was no  
300 correlation between genetic diversity and habitat distance ( $r = 0.13$ ,  $p = 0.500$ ) (Fig. 3).

301 The predictor variable of most importance after model averaging and the only variable to  
302 exceed the cutoff of 0.6 was occupancy, with a relative importance of 0.74 (Fig. 4). Using only  
303 occupancy as a predictor in our final model results in  $p = 0.008$  with coefficient =  $8.7 \times 10^{-5}$ .  
304 This small coefficient likely reflects difference in scale between heterozygosity and occupancy,  
305 rather than minor effect size; scaling genetic diversity to the same order of magnitude as the  
306 occupancy data results in a corresponding increase in the response of genetic diversity to changes  
307 in occupancy (in other words, an increase in the regression coefficient; coefficient after scaling  
308 genetic diversity = 0.870).

309 The rRMSE calculated for the prediction of species abundance based on heterozygosity was  
310 0.55, with an  $r = 0.4$  and  $p = 0.02$ . These values are somewhat comparable to those reported in  
311 Yin and He (2014), but suggest a reduced predictive power for genetic diversity compared to  
312 statistical models based on occupancy and spatial distribution. However, the data used for  
313 validation of the models summarized in Yin and He (2014) are from an area of  $1 \text{ km}^2$ , whereas  
314 the current study is still able to recover a significant correlation between observed and predicted  
315 abundance estimates from a study region of  $2350 \text{ km}^2$  (maximum distance between sites = 38.4  
316 km). Nonetheless, a sliding-window resampling analysis of abundance data demonstrates that a  
317 single day of sampling can generate a stronger correlation with long-term abundance than  
318 genetic diversity (Fig. 5A). Moreover, only three days of sampling are required to produce a  
319 stronger correlation with occupancy (Fig. 5B).

320

## 321 DISCUSSION

322

323 We recovered a significant positive relationship between genetic diversity and empirical  
324 estimates of species abundance and occupancy, with occupancy being the most significant  
325 predictor of nucleotide diversity. While occupancy is correlated with patterns of habitat use

326 among species, we find that direct measures of habitat specialization were not significant  
327 predictors of genetic diversity. Importantly, our results suggest that genetic diversity is at least a  
328 weak proxy for species abundance in the regional community. Additionally, we show a strong,  
329 positive relationship between occupancy and abundance, lending further support to a classic  
330 ecological relationship recovered for many taxa but rarely examined in squamates (Gaston et al.  
331 2002; Gaston et al. 1997; Freckleton et al. 2005). The pervasiveness of this relationship in  
332 macroecology suggests a mechanism linking changes in population dynamics at local and  
333 regional scales (Freckleton et al. 2005).

334 Our study reveals that a species rich community of related taxa displays the same positive  
335 diversity-abundance association found by other studies at both narrower and broader  
336 phylogenetic and geographic scales. The proportion of variance in genetic diversity that was  
337 explained by local-scale abundance in the present study is similar to that explained by museum  
338 occurrence records (a proxy for global population size) in a recent study of genetic diversity in  
339 the lizard genus *Ctenotus*, a member of the Sphenomorphine clade that is represented in the  
340 current dataset (Singhal et al. 2017b). Similarly, Pearson correlations between abundance and  
341 diversity recovered from broader phylogenetic sampling and meta-analyses in other taxa are also  
342 comparable to the correlation recovered here ( $r = 0.4$ ) (Leimu et al. 2006; McCusker and  
343 Bentzen 2010). It is useful to discover that genetic diversity retains at least some predictive  
344 power for population size across these different scales.

345 However, much of the variation in genetic diversity among species is unexplained by  
346 abundance and occupancy. With respect to predicting total abundance (e.g., pooled across all  
347 survey years), we found that genetic variation was equivalent to just a single "average" day of  
348 sampling at Matuwa (Fig. 5). These results suggest that nucleotide diversity is heavily influenced  
349 by factors other than census population size, or that ecological sampling in this community is  
350 unable to capture true population size. Interpreting results from ecological analyses may help to  
351 clarify this issue. For example, habitat specialists may be locally abundant given non-random site  
352 selection, with low heterozygosity indicative of lower regional abundance. Although the most  
353 abundant species in this community also tend to be the most widespread, some high- and mid-  
354 abundance species of the sphenomorphine clade exhibit relatively low occupancy, in addition to  
355 a higher degree of habitat specialization. Assuming occupancy at the chosen sites is to some  
356 degree correlated with population connectivity, these observations suggest that gene flow could

357 be mediated by habitat preference, restricting individuals to certain microhabitats and preventing  
358 movement through sub-optimal patches across large areas of landscape (Wang and Bradburd  
359 2014). Concordantly, Pianka (2014) found that many of the most abundant species, as measured  
360 over 42 years in broadly the same region as the current study, are also the most restricted in  
361 dietary and microhabitat niche breadth. However, because occupancy at Matuwa is strongly  
362 correlated with both abundance and habitat generalism, the wide range of heterozygosity values  
363 exhibited by species at the upper range of occupancy suggest that other processes not evaluated  
364 by this study may constrain heterozygosity in these taxa. For example, the relationship between  
365 abundance and genetic diversity can be weakened by past demographic processes such as  
366 bottlenecks or range expansions not reflected by current population size (Excoffier and Ray  
367 2008; Banks et al. 2013; Dalongeville et al. 2016).

368 Similarly, because the chosen sample sites are not strictly a random draw from the  
369 landscape, there is no guarantee that ecological sampling at the community level is sufficient to  
370 accurately track true variation in population size. It may therefore be the case that occupancy is a  
371 more reliable estimate of long-term abundance than the pooled abundance measurements  
372 reported here. Population size will fluctuate through time, and abundance data are likely to be  
373 susceptible to noise generated by detection bias or recapture of individuals. While this is also  
374 true for occupancy data, occupancy provides a more coarse-grained metric that could be more  
375 sensitive to increases in relative species abundance or to the number of subpopulations in the  
376 region. Occupancy in a regional and community context may thereby provide a more robust  
377 proxy for true population size relative to other species in a comparative analysis.

378

## 379 CONCLUSION

380 The results of this study support our initial prediction that greater abundance would  
381 correlate with higher levels of genetic diversity, and further suggest that factors associated with  
382 landscape occupancy contribute to observed variation in heterozygosity. Our study provides  
383 evidence that genetic diversity is at least weakly informative about demographic processes  
384 occurring at phylogenetic scales broader than conspecific populations. However, genetic  
385 diversity does no better at predicting species abundance, as measured in the community at  
386 Matuwa, than a single "average" day of standardized sampling, and does only marginally better  
387 at predicting occupancy. Whether these results reflect a failure of genetic diversity or ecological

388 sampling to adequately capture variation in true census population size remains unknown. In  
389 conclusion, patterns of intraspecific genetic diversity potentially can serve as proxies for  
390 regional-scale species abundance, but further evidence from diverse communities is needed,  
391 ideally incorporating information on species abundance through time (Magurran 2007). More  
392 broadly, our study provides further evidence for Lewontin's paradox and suggests that resolving  
393 the paradox may require further understanding and consideration of the relationship between  
394 historical demography and present-day census-size.

395

396

#### 397 ACKNOWLEDGEMENTS

398

399 We thank C. Dardia, A. Davis Rabosky, P. Doughty, I. Kealley, G. Schneider, D. Stefoni,  
400 P. Title, and the staff of the Kalgoorlie office of the Department of Biodiversity, Conservation  
401 and Attractions for logistical assistance associated with fieldwork and sample acquisition. We  
402 gratefully acknowledge the Martu, the Traditional Owners of Matuwa, for access to their lands  
403 and for supporting our fieldwork. For technical advice and logistical support we thank Allison  
404 Devault and Jake Enk from MYcroarray, R. Marchan Rivadneira, and R. Murrell.

405

406 This work was supported by NSF grants OSIE-0612855, DEB-0814277, DEB-1754398, and by a  
407 fellowship to DLR from the David and Lucile Packard Foundation. SS was supported by a NSF  
408 DEB-1519732.

409

410 Field sampling at Matuwa was conducted under permit SF0004654 to DLR (Western Australian  
411 Department of Parks and Wildlife).

412

#### 413 DATA ACCESSIBILITY

414 Raw reads are associated with BioProject PRJNA518083, and additional data are available in a  
415 dryad digital repository (doi:10.5061/dryad.3b1rj70).

#### 416 AUTHOR CONTRIBUTIONS

417 MRG and DLR designed the study, analyzed data, and wrote the paper. MRG and SS conducted  
418 lab work. SS contributed analytical tools. MAC and DLR conducted fieldwork.

419 CONFLICT OF INTEREST

420 The authors have no conflicts of interest to declare.

421 FIGURE LEGENDS

422 Figure 1. (A) Bootstrapped estimates of heterozygosity across four species of Matuwa lizards, as  
423 a function of the number of loci used to compute the estimate. Genome-wide heterozygosity  
424 converges rapidly to a limiting value and can be robustly estimated from samples of 500 or more  
425 loci. Species illustrated include *Diplodactylus pulcher*, *Lerista timida*, *Moloch horridus*, and  
426 *Morethia ruficauda*. Also drawn are the 95% confidence intervals around the estimated mean  
427 heterozygosity for each species, shown as a grey dotted line, as measured across all loci. (B)  
428 Genome-wide estimates of heterozygosity are highly correlated across conspecifics. Each point  
429 represents the pairwise relationship between heterozygosity estimates from two individual lizards  
430 of a given species. Dotted line illustrates isometric scaling relationship.

431

432 Figure 2. Phylogenetic distribution of occupancy, abundance, and heterozygosity across 30  
433 species of lizards from Matuwa. Abundance at each of 24 sites is represented by the size of the  
434 point, and within-species genetic diversity is represented by color. Occupancy is simply the  
435 number of sites at which a species was detected (e.g., empty "cells" denote absence).

436 Corresponding abundance data can be found in Table S1.

437

438 Figure 3. Correlation matrix showing relationships between genetic diversity and four predictor  
439 variables: log abundance, occupancy, body size as measured by snout-vent length, and a metric  
440 of habitat specialization (habitat distance) wherein larger values indicate generalist species and  
441 vice versa. Regression lines and phylogenetic  $p$ -values are shown for significant relationships,  
442 and points are colored in greyscale by clade.

443

444 Figure 4. Results from model averaging, showing the relative importance of each independent  
445 variable for predicting within-species genetic diversity. Also shown are the coefficient sign and  
446 significance from the final phylogenetic linear model including occupancy, the only variable to  
447 exceed the cutoff value of 0.6 relative importance.

448

449 Figure 5. Expected correlation in abundance (A) and occupancy (B) between cumulative survey  
450 totals and a specified survey duration (x-axis). For example, a value of  $x = 20$  gives the expected  
451 correlation between two estimates of the species abundance distributions: the cumulative (133  
452 day) survey totals, versus a shorter interval of 20 consecutive survey days. A value of  $x = 1$   
453 indicates the extent to which a single day of sampling would have estimated cumulative  
454 abundance and occupancy totals. The observed correlation of genetic diversity with abundance  
455 and occupancy is illustrated by the corresponding horizontal dotted lines in each panel. Genetic  
456 diversity predicts overall species abundance with a correlation slightly below that obtained from  
457 one day of sampling, and it predicts species occupancy with a correlation slightly below that  
458 obtained from three days of sampling.

459

460 Table S1. Abundance data for each species across sites at Matuwa, corresponding to Figure 2.

#### 461 REFERENCES

- 462 Aljanabi, S. M., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality  
463 genomic DNA for PCR-based techniques. *Nucleic acids research* 25(22), 4692-4693.
- 464 Anderson, D. R., & Burnham, K. P. (2002). Avoiding pitfalls when using information-theoretic  
465 methods. *The Journal of Wildlife Management*, 912-918.
- 466 Banks, S. C., Cary, G. J., Smith, A. L., Davies, I. D., Driscoll, D. A., Gill, A. M., Lindenmayer,  
467 D. B., & Peakall, R. (2013). How does ecological disturbance influence genetic diversity?  
468 *Trends in Ecology & Evolution*, 28(11), 670-679.
- 469 Bazin, E., Glémin, S., & Galtier, N. (2006). Population size does not influence mitochondrial  
470 genetic diversity in animals. *Science*, 312(5773), 570.
- 471 Begun, D. J., Holloway, A. K., Stevens, K., Hillier, L. W., Poh, Y.-P., Hahn, M. W., Nista, P. M.,  
472 Jones, C. D., Kern, A. D., Dewey, C. N., Pachter, L., Myers, E., & Langley, C. H. (2007).  
473 Population genomics: whole-genome analysis of polymorphism and divergence in *Drosophila*  
474 *simulans*. *PLOS Biology*, 5(11), e310.
- 475 Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T., & Rasplus, J. Y. (2004). Specialization  
476 and habitat: spatial and environmental effects on abundance and genetic diversity of forest  
477 generalist and specialist *Carabus* species. *Molecular Ecology*, 13(7), 1815-1826.



478 Brouat, C., Sennedot, F., Audiot, P., Leblois, R., & Rasplus, J. Y. (2003). Fine-scale genetic  
479 structure of two carabid species with contrasted levels of habitat specialization. *Molecular*  
480 *Ecology*, *12*(7), 1731-1745.

481 Charlesworth, B. (2009). Effective population size and patterns of molecular evolution and  
482 variation. *Nature Reviews Genetics*, *10*, 195.

483 Corbett-Detig, R. B., Hartl, D. L., & Sackton, T.B. (2015). Natural selection constrains neutral  
484 diversity across a wide range of species. *PLoS Biology*, *13*(4), e1002112.

485 Cowan, M. A., Edinger, D., & Coate, K. (2017). Biodiversity in the southern rangelands:  
486 variation in biota over time and space on the Black Range and Lake Mason stations, Murchison  
487 Bioregion, Western Australia. *Conservation Science Western Australia*, *12*(1).

488 Dalongeville, A., Andrello, M., Mouillot, D., Albouy, C., & Manel, S. (2016). Ecological traits  
489 shape genetic diversity patterns across the Mediterranean Sea: a quantitative review on fishes.  
490 *Journal of Biogeography*, *43*(4), 845-857.

491 Devillard, S., Santin-Janin, H., Say, L., & Pontier, D. (2011). Linking genetic diversity and  
492 temporal fluctuations in population abundance of the introduced feral cat (*Felis silvestris catus*)  
493 on the Kerguelen archipelago. *Molecular Ecology*, *20*(24), 5141-5153.

494 Ellegren, H., & Galtier, N. (2016). Determinants of genetic diversity. *Nature Reviews Genetics*,  
495 *17*(7), 422.

496 Excoffier, L., & Ray, N. (2008). Surfing during population expansions promotes genetic  
497 revolutions and structuration. *Trends in Ecology and Evolution*, *23*(7), 347-351.

498 Faircloth, B. C., McCormack, J. E., Crawford, N. G., Harvey, M. G., Brumfield, R. T., & Glenn,  
499 T. C. (2012). Ultraconserved elements anchor thousands of genetic markers spanning multiple  
500 evolutionary timescales. *Systematic Biology*, *61*(5), 717-726.

501 Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: a  
502 review. *Genetics Research*, *66*(2), 95-107.

503 Freckleton, R. P., Noble, D., & Webb, T. J. (2005). Distributions of habitat suitability and the  
504 abundance-occupancy relationship. *The American Naturalist*, *167*(2), 260-275.

505 Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M., & Lawton, J.  
506 H. (2002). Abundance-occupancy relationships. *Journal of Applied Ecology*, *37*(s1), 39-59.

507 Gaston, K. J., Blackburn, T. M., & Lawton, J. H. (1999.) Interspecific abundance-range size  
508 relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, *66*(4), 579-601.

509 Godt, M. J. W., Johnson, B. R., & Hamrick, J. L. (1996). Genetic diversity and population size in  
510 four rare southern Appalachian plant species. *Conservation Biology*, *10*(3), 796-805.

511 Gotelli, N. J., & Chao, A. (2013). Measuring and estimating species richness, species diversity,  
512 and biotic similarity from sampling data. In *The Encyclopedia of Biodiversity*, Vol. 5, ed. SA  
513 Levin, pp. 195–211. Waltham, MA: Academic. 2nd ed.

514 Grundler, M. R., Pianka, E. R., Pelegrin, N., Cowan, M. A., & Rabosky, D. L. (2017). Stable  
515 isotope ecology of a hyper-diverse community of scincid lizards from arid Australia. *PloS one*,  
516 *12*(2), e0172879.

517 Hague, M. T. J., & Routman, E. J. (2016). Does population size affect genetic diversity? A test  
518 with sympatric lizard species. *Heredity*, *116*(1), 92-98.

519 Harvey, M. G., Aleixo, A., Ribas, C. C., & Brumfield, R. T. (2017). Habitat association predicts  
520 genetic diversity and population divergence in Amazonian birds. *The American Naturalist*,  
521 *190*(5), 631-648.

522 He, F., & Gaston, K. J. (2000). Estimating species abundance from occurrence. *The American*  
523 *Naturalist*, *156*(5), 553-559.

524 Yun H., Ramachandran, A., Hwu, W.-M., Ma, J., & Chen, D. (2016). BLESS 2: accurate,  
525 memory-efficient and fast error correction method. *Bioinformatics*, *32*(15), 2369-2371.

526 Ho, L. S. T., Ane, C., Lachlan, R., Tarpinian, K., Feldman, R., Yu, Q., van der Bijl, W., & Ho, M.  
527 L. S. T. (2018). Package ‘phylolm’.

528 Ishiyama, N., Koizumi, I., Yuta, T., & Nakamura, F. (2015). Differential effects of spatial  
529 network structure and scale on population size and genetic diversity of the ninespine stickleback  
530 in a remnant wetland system. *Freshwater biology*, *60*(4), 733-744.

531 James, C. D., & Shine, R. (2000). Why are there so many coexisting species of lizards in  
532 Australian deserts? *Oecologia*, *125*(1), 127-141.

533 Jackson, N. D., & Fahrig, L. (2014). Landscape context affects genetic diversity at a much larger  
534 spatial extent than population abundance. *Ecology*, *95*(4), 871-881.

535 VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and the  
536 environmental niche: environmental suitability estimated from niche models predicts the upper  
537 limit of local abundance. *The American Naturalist*, *174*(2), 282-291.

538 Khimoun, A., Eraud, C., Ollivier, A., Arnoux, E., Rocheteau, V., Bely, M., Lefol, E., Delpuech,  
539 M., Carpentier, M. L., & Leblond, G. (2016). Habitat specialization predicts genetic response to  
540 fragmentation in tropical birds. *Molecular Ecology*, 25(16), 3831-3844.

541 Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of  
542 gene flow. *The American Naturalist*, 175(3), 316-334.

543 Leffler, E. M., Bullaughey, K., Matute, D. R., Meyer, W. K., Ségurel, L., Venkat, A., Andolfatto,  
544 P., & Przeworski, M. (2012). Revisiting an old riddle: what determines genetic diversity levels  
545 within species? *PLOS Biology*, 10(9), e1001388.

546 Leimu, R., Mutikainen, P., Koricheva, J., & Fischer, M. (2006). How general are positive  
547 relationships between plant population size, fitness and genetic variation? *Journal of Ecology*,  
548 94(5), 942-952.

549 Lewontin, R. C. (1972). The apportionment of human diversity. In *Evolutionary biology*, (pp.  
550 381-398). Springer, Boston, MA.

551 Li, H., & Durbin, R. (2011). Inference of human population history from individual whole-  
552 genome sequences. *Nature*, 475(7357), 493.

553 Lozier, J. D. (2014). Revisiting comparisons of genetic diversity in stable and declining species:  
554 assessing genome-wide polymorphism in North American bumble bees using RAD sequencing.  
555 *Molecular Ecology*, 23(4), 788-801.

556 Magurran, A. E. (2007). Species abundance distributions over time. *Ecology Letters*, 10, 347-354.

557 Magurran, A. E., Baillie, S.R., Buckland, S.T., Dick, J. M., Elston, D. A., Scott, E. M., Smith, R.  
558 I., Somerfield, P. J., & Watt, A. D. (2010). Long-term datasets in biodiversity research and  
559 monitoring: assessing change in ecological communities through time. *Trends in Ecology &*  
560 *Evolution*, 25(10), 574-582.

561 Manly, B. F. J. (1996). Are there clumps in body-size distributions? *Ecology*, 77(1), 81-86.

562 McCusker, M. R., & Bentzen, P. (2010). Positive relationships between genetic diversity and  
563 abundance in fishes. *Molecular Ecology*, 19(22), 4852-4862.

564 McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas,  
565 M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer,  
566 B. A., Ostling, A., Soykan, C. U., Ugland, K. I., & White, E. P. (2007). Species abundance  
567 distributions: moving beyond single prediction theories to integration within an ecological  
568 framework. *Ecology Letters*, 10(10), 995-1015.

569 Mesquita, D. O., Costa, G. C., Colli, G. R., Costa, T. B., Shepard, D. B., Vitt, L. J., & Pianka, E.  
570 R. (2016). Life-history patterns of lizards of the world. *The American Naturalist*, 187(6), 689-  
571 705.

572 Meyer, C. F. J., Aguiar, L. M. S., Aguirre, L. F., Baumgarten, J., Clarke, F. M., Cosson, J.-F.,  
573 Villegas, S. E., Fahr, J., Faria, D., Furey, N., Henry, M., Hodgkison, R., Jenkins, R. K. B., Jung,  
574 K. G., Kingston, T., Kunz, T. H., MacSwiney Gonzalez, M. C., Moya, I., Pons, J.-M., Racey, P.  
575 A, Rex, K., Sampaio, E. M., Stoner, K. E., Voigt, C. C., von Staden, D., Weise, C. D., & Kalko,  
576 E. K. V. (2010). Long-term monitoring of tropical bats for anthropogenic impact assessment:  
577 Gauging the statistical power to detect population change. *Biological Conservation*, 143(11),  
578 2797-2807.

579 Morton, S. R., & James, C.D. (1988). The diversity and abundance of lizards in arid Australia: a  
580 new hypothesis. *The American Naturalist*, 132(2), 237-256.

581 Nazareno, A. G., Bemmels, J. B., Dick, C. W., & Lohmann, L. G. (2017). Minimum sample sizes  
582 for population genomics: an empirical study from an Amazonian plant species. *Molecular*  
583 *Ecology Resources*, 17, 1136-1147.

584 Ortego, J., Aparicio, J. M., Cordero, P. J., & Calabuig, G. (2008). Individual genetic diversity  
585 correlates with the size and spatial isolation of natal colonies in a bird metapopulation.  
586 *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1646), 2039-2047.

587 Palstra, F. P., & Ruzzante, D. E. (2008). Genetic estimates of contemporary effective population  
588 size: what can they tell us about the importance of genetic stochasticity for wild population  
589 persistence? *Molecular Ecology*, 17, 3428-3447.

590 Patton, J. L., & Yang, S. Y. (1977). Genetic variation in *Thomomys bottae* pocket gophers:  
591 macrogeographic patterns. *Evolution*, 31(4), 697-720.

592 Pearce, J. and Ferrier, S. (2001). The practical value of modelling relative abundance of species  
593 for regional conservation planning: a case study. *Biological Conservation*, 98(1), 33-43.

594 Pianka, E. R. (1972). Zoogeography and speciation of Australian desert lizards: an ecological  
595 perspective. *Copeia*, 8, 127-145.

596 Pianka, E. R. (1986). Ecology and natural history of desert lizards: analyses of the ecological  
597 niche and community structure. 208 pp, Princeton University Press, New Jersey, USA.

598 Pianka, E. R. (2014). Rarity in Australian desert lizards. *Austral Ecology*, 39(2), 214-224.

599 Pierson, J., Luikart, G., & Schwartz, M. (2015). The application of genetic indicators in wild  
600 populations: potential and pitfalls for genetic monitoring. *Indicators and Surrogates of*  
601 *Biodiversity and Environmental Change*, 149.

602 Pierson, J. C., Graves, T. A., Banks, S. C., Kendall, K. C., & Lindenmayer, D. B. (2018).  
603 Relationship between effective and demographic population size in continuously distributed  
604 populations. *Evolutionary Applications*.

605 Pinsky, M. L., & Palumbi, S. R. (2014). Meta-analysis reveals lower genetic diversity in  
606 overfished populations. *Molecular Ecology*, 23(1), 29-39.

607 Rabosky, D. L., Cowan, M. A., Talaba, A. L., & Lovette, I. J. (2011). Species interactions  
608 mediate phylogenetic community structure in a hyperdiverse lizard assemblage from arid  
609 Australia. *The American Naturalist*, 178(5), 579-595.

610 Rabosky, D. L., Reid, J., Cowan, M. A., & Foulkes, J. (2007). Overdispersion of body size in  
611 Australian desert lizard communities at local scales only: no evidence for the Narcissus effect.  
612 *Oecologia*, 154(3), 561-570.

613 Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-  
614 Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L.,  
615 Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte,  
616 D., Nagy, Z. T., Nogueira, C. d. C., Pauwels, O. S. G., Pincheira-Donoso, D., Powney, G. D.,  
617 Sindaco, R., Tallowin, O. J. S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P.,  
618 Wang, Y., Orme, C. D. L., Grenyer, R., & Meiri, S. (2017). The global distribution of tetrapods  
619 reveals a need for targeted reptile conservation. *Nature Ecology & Evolution*, 1(11), 1677-1682.

620 Romiguier, J., Gayral, P., Ballenghien, M., Bernard, A., Cahais, V., Chenuil, A., Chiari, Y.,  
621 Dernet, R., Duret, L., Faivre, N., Loire, E., Lourenco, J. M., Nabholz, B., Roux, C.,  
622 Tsagkogeorga, G., Weber, A. a. T., Weinert, L. A., Belkhir, K., Bierne, N., Glémin, S., &  
623 Galtier, N. (2014). Comparative population genomics in animals uncovers the determinants of  
624 genetic diversity. *Nature*, 515(7526), 261-263.

625 Schwartz, M. K., Luikart, G., & Waples, R. S. (2007). Genetic monitoring as a promising tool for  
626 conservation and management. *Trends in ecology & evolution*, 22(1), 25-33.

627 Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density  
628 estimators for home range analysis. *Ecology*, 77(7), 2075-2085.

629 Singhal, S., Grundler, M., Colli, G., & Rabosky, D. L. (2017a). Squamate Conserved Loci (Sq  
630 CL): a unified set of conserved loci for phylogenomics and population genetics of squamate  
631 reptiles. *Molecular ecology resources*, 17(6), e12-e24.

632 Singhal, S., Huang, H., Title, P. O., Donnellan, S. C., Holmes, I., & Rabosky, D. L. (2017b).  
633 Genetic diversity is largely unpredictable but scales with museum occurrences in a species-rich  
634 clade of Australian lizards. *Proceedings of the Royal Society B: Biological sciences*, 284(1854),  
635 20162588.

636 Stangel, P. W., Lennartz, M. R., & Smith, M. H. (1992). Genetic variation and population  
637 structure of red-cockaded woodpeckers. *Conservation Biology*, 6(2), 283-292.

638 Sun, M. (1996). Effects of population size, mating system, and evolutionary origin on genetic  
639 diversity in *Spiranthes sinensis* and *S. hongkongensis*. *Conservation Biology*, 10(3), 785-795.

640 Tajima, F. (1983). Evolutionary relationship of DNA sequences in finite populations. *Genetics*,  
641 105(2), 437-460.

642 Tallmon, D. A., Gregovich, D., Waples, R. S., Baker, C. S., Jackson, J., Taylor, B. L., Archer, E.,  
643 Martien, K. K., Allendorf, F. W., & Schwartz, M. K. (2010). When are genetic methods useful  
644 for estimating contemporary abundance and detecting population trends? *Molecular Ecology*  
645 *Resources*, 10(4), 684-692.

646 Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled  
647 phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*,  
648 204, 23-31.

649 Wagner, C. E., Harmon, L. J., & Seehausen, O. (2012). Ecological opportunity and sexual  
650 selection together predict adaptive radiation. *Nature*, 487(7407), 366.

651 Wang, I. J., & Bradburd, G. S. (2014). Isolation by environment. *Molecular Ecology*, 23(23),  
652 5649-5662.

653 White, E. P., Ernest, S. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body  
654 size and abundance in ecology. *Trends in ecology & evolution*, 22(6), 323-330.

655 Willing, E.-M., Dreyer, C., & Van Oosterhout, C. (2012). Estimates of genetic differentiation  
656 measured by FST do not necessarily require large sample sizes when using many SNP markers.  
657 *PloS one*, 7(8), e42649.

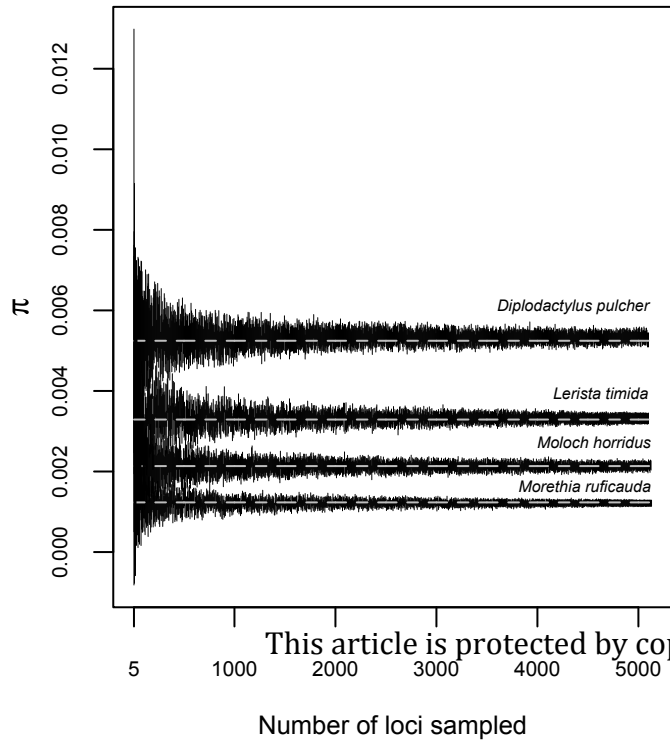
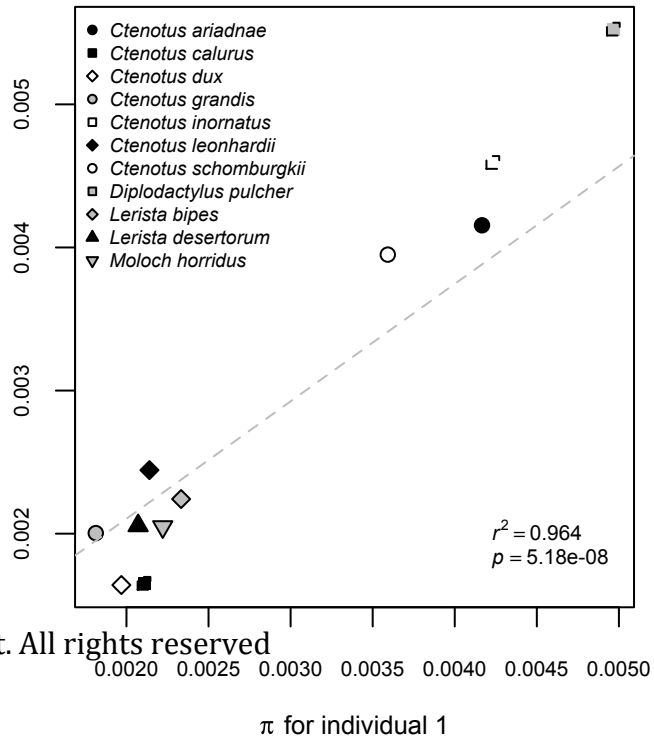
658 Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., &  
659 Warren, P. H. (2005). Body size in ecological networks. *Trends in ecology & evolution* 20(7),  
660 402-409.

661 Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16(2), 97.

662 Yin, D., & He, F. (2014). A simple method for estimating species abundance from occurrence  
663 maps. *Methods in Ecology and Evolution*, 5(4), 336-343.

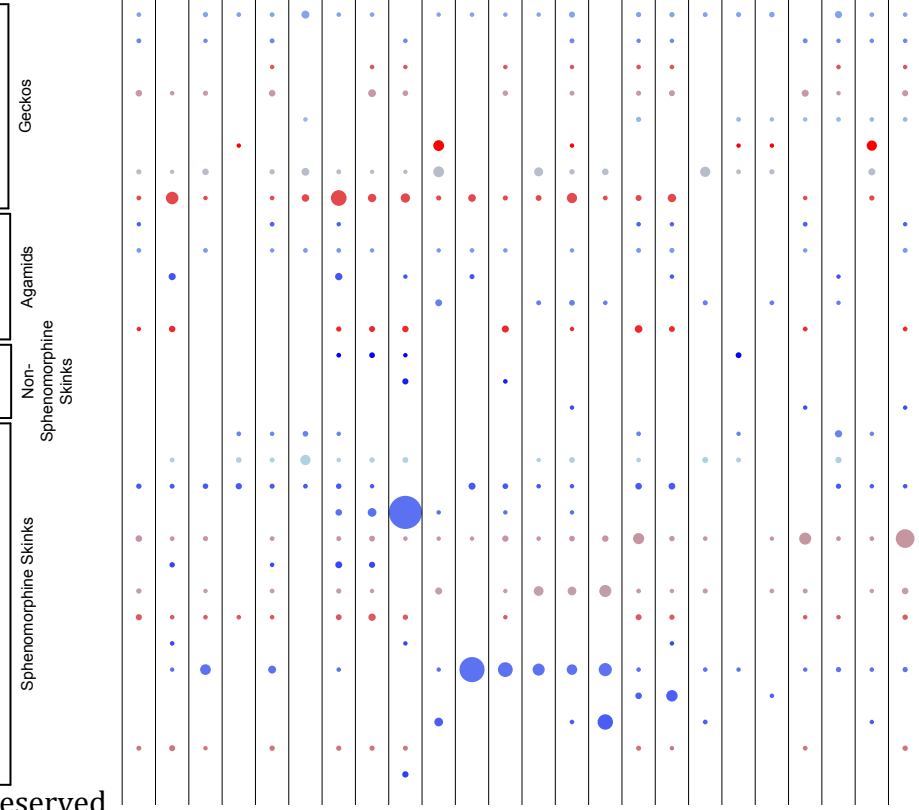
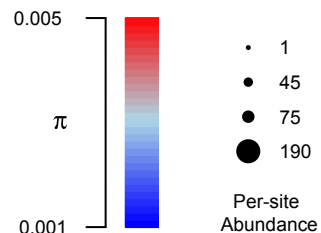
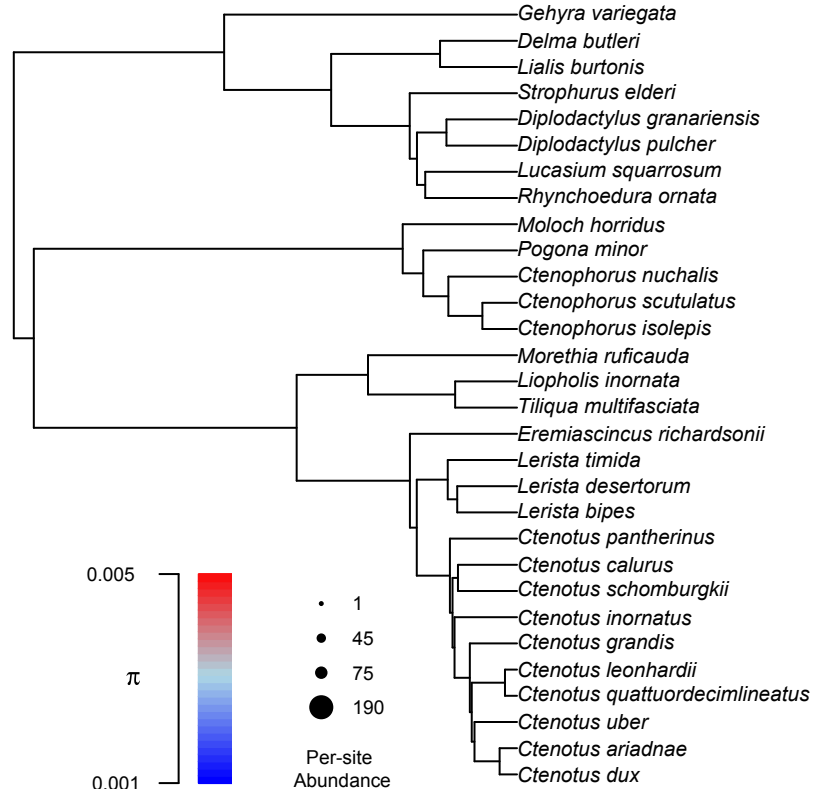
Author Manuscript

(A)

 $\pi$  for individual 2 $\pi$  for individual 1

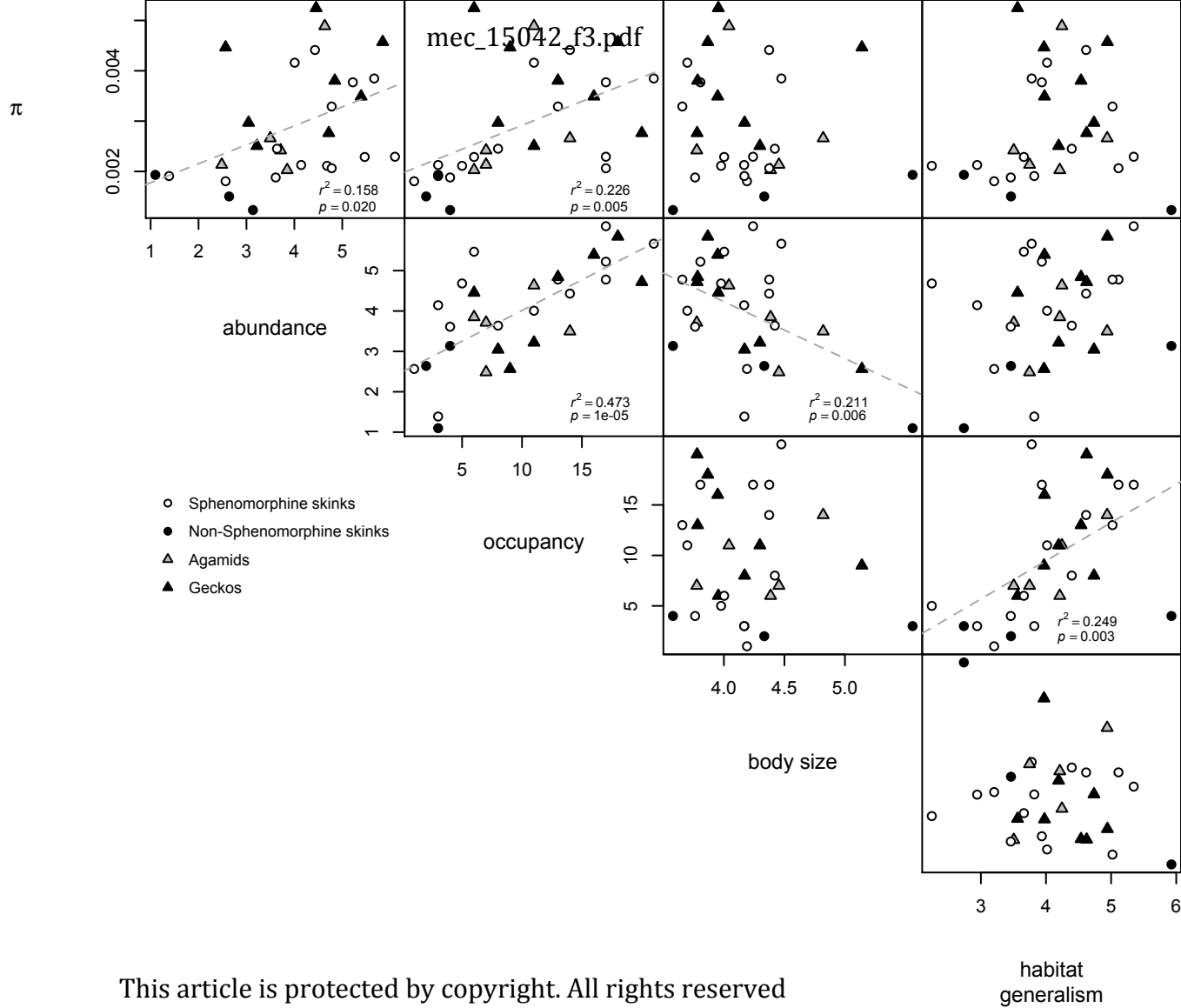


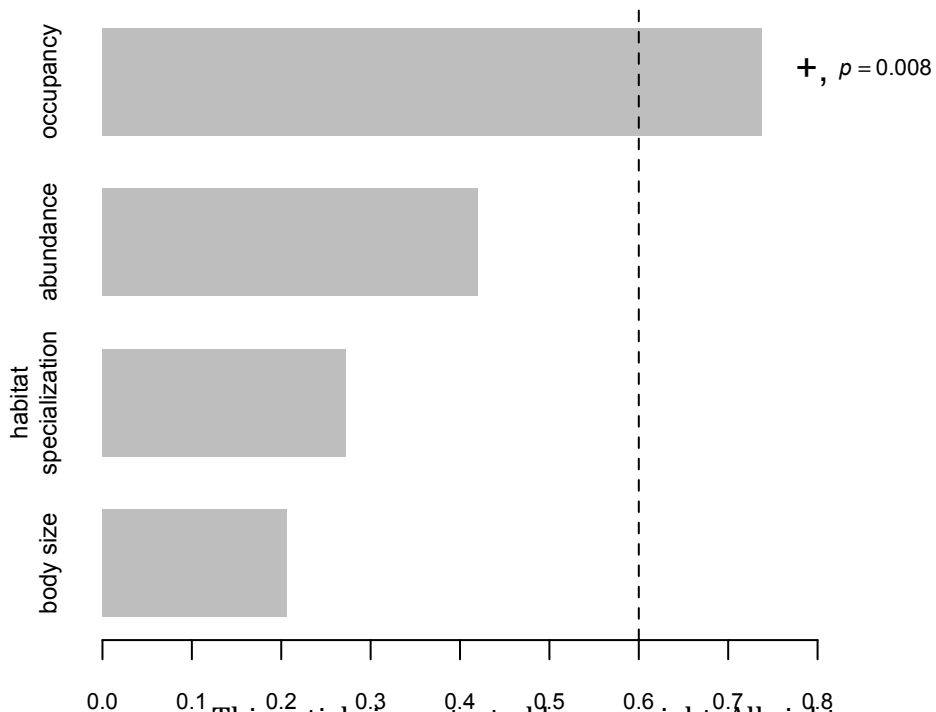
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24



This article is protected by copyright. All rights reserved

Abundance across sites at Matuwa





This article is protected by copyright. All rights reserved

Relative Importance

Pearson correlation with total survey abundance

0.0 0.2 0.4 0.6 0.8 1.0

