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Covariation between intraspecific genetic diversity and species diversity within a plant functional group

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Running title: Covariation between species and genetic diversity

Summary

1. Species diversity and genetic diversity are fundamental components of biodiversity. A primary goal of biodiversity studies is to explain the distribution of species and alleles in space and time. A new challenge is to cross discipline boundaries and explore the relationship between these two scales of diversity.
2. In the biodiverse northern sandplain shrublands of southwestern Australia, the woody shrub *Banksia attenuata* occurs on patchily distributed sand dunes, and coexists with *B. hookeriana*, *B. menziesii*, and two small tree species, *Eucalyptus todtiana* and *Xylomelum angustifolium*, which together comprise a plant functional group of large shrubs/small trees.
3. Genetic variation (alleles per locus and heterozygosity) between 736 *B. attenuata* individuals on 27 discrete dunes was assessed using 11 polymorphic microsatellite markers. For each dune, the physical properties of area and height, and species diversity (richness and evenness) of the functional group, were measured.
4. Synthesis: Genetic diversity of *B. attenuata* covaried positively with species diversity, which in turn covaried strongly with dune height rather than dune area. The positive relationship between species and genetic diversity demonstrated here supports the theory of common environmental, rather than neutral, processes acting directly or indirectly on both scales of diversity, and suggests the possibility of predicting one component of diversity on the basis

of the other.

Key-words: *Banksia*, *Eucalyptus*, environmental gradients, functional group, genetic diversity, metapopulation, path analysis, species diversity.

Introduction

Genetic diversity and species diversity are two fundamental components of biodiversity. Antonovics (1976, 2003) suggests that the environmental and evolutionary forces accounting for species diversity and genetic diversity are similar. The processes assumed to shape community assemblages in niche-oriented models, and species co-existing via heterogeneous patches and migration, also have evolutionary analogues in natural selection and gene flow (Vellend 2003, 2005; Alonso *et al.* 2006). A major goal of studies on species diversity is to explain the observed patterns of species abundance in space and time, and across scales (Ricklefs & Schluter 1993; Chave 2004). Similarly, studies on population genetic diversity also try to explain the observed patterns of allelic abundance in space and time, and across scales (Alonso *et al.* 2006). Research synthesizing the disciplines of community ecology and population genetics provides a unifying perspective at the levels of genes and species, helping to advance our understanding of the nature of biodiversity (Antonovics 1976; Bell 2001; Vellend 2005).

The idea that the forces accounting for given levels of species diversity and genetic diversity are similar has existed for decades (Antonovics 1976). Vellend (2003, 2005) showed that the species-genetic diversity correlation (SGDC) was generally positive, and such a correlation was consistent with island biogeography

theory, depending on size of the reference area, immigration rates and environmental heterogeneity. In addition, Hubbell (2001) proposed the neutral theory of community ecology that is largely analogous to the theory of neutral genetic variation. Consequently, Vellend & Geber (2005) suggested that the parallel action of neutral processes on the two scales of diversity is also a parsimonious explanation for positive species–genetic diversity relationships if such pattern could not be correlated with environmental and selection processes. While this notion has been discussed in recent theoretical papers, supporting empirical evidence which takes into account possible effects of environmental properties, is limited. For instance, Booth & Grime (2003) found that Shannon-Weiner species diversity increased, although not significantly, with the number of genotypes in experimental communities. Cleary *et al.* (2006) revealed a strong correlation between species and allelic richness of butterfly communities across rainforest habitats, some of which were affected by fire. They suggested that environmental ‘regimes’, habitat discontinuities and dispersal limitations may have accounted for the shared patterns although they did not seek any associated environmental gradients. A positive correlation was also found between trans-specific genetic diversity per species for three isozyme-gene systems and plant species diversity in forest tree communities, without suggesting an explanation (Wehenkel *et al.* 2006). However, Karlin *et al.* (1984) derived a negative correlation between the two levels of diversity that they related to the effects of differences in elevation.

It is usually impossible to study all species living in an ecosystem simultaneously, and a common practice in both theoretical and empirical ecology is to examine complex natural communities in terms of functional groups. This practice presumes that all species within a group are more similar in their effects on population,

community, or ecosystem processes than they are to the species from another group (e.g. Symstad 2000). This approach is particularly pertinent for research in species-rich systems such as that reported on here.

We assessed covariations between intraspecific (population genetic) diversity in a metapopulation of *Banksia attenuata* with species richness of the coincident putative community functional group to which *B. attenuata* belongs, and associated habitat variation in the biodiverse northern sandplain shrublands of the South-Western Australian Floristic Region. This region exhibits high levels of species diversity at the point, community and landscape scales (Hopper & Gioia 2004), and is recognized as an international biodiversity hotspot (Myers *et al.* 2002), with an estimated 7380 plant species. Our objective was to test the hypothesis that parallel processes acting on species diversity and genetic diversity could result in positive covariation between these two measures. We first tested the hypothesis of a positive species diversity-genetic diversity correlation (SGDC; Antonovics 1976; Vellend 2003). Then we tested the relative importance of dune height (a surrogate for water availability; Enright & Lamont 1992) and habitat area, which has been hypothesized as one of the most important driving forces for positive SGDC (Vellend 2003). Finally, we explored the possible causative relationships between habitat properties, species diversity and genetic diversity.

Materials and Methods

The study area of $3 \times 4 \text{ km}^2$ is described in He *et al.* (2004) and Calviño-Cancela *et al.* (2008). Mean annual rainfall is 510 mm, mostly falling in winter-spring (May-November), with mean temperatures in the warmest month (February) of 29°C , and temperatures $> 45^\circ\text{C}$ often reached in summer-autumn. The soil substrate in the

study and surrounding area is an unconsolidated sand overlying silt-clay at depths of 0.5 to 10 m, forming an undulating landscape of sand dune ‘islands’ and intervening swales. Sand depth is the main determinant of the distribution of most species (Hnatiuk & Hopkins 1981, Lamont *et al.* 1989). All *Banksia* species in the study area are restricted to the dunes (i.e. absent from the swales), with populations connected through gene flow, via seeds and pollen (He *et al.* 2004).

We assessed the distribution and abundance of the five largest nonclonal, shrub-tree species that formed a deep rooted, large shrub – small tree, plant functional group in the study area: *Banksia attenuata*, *B. hookeriana*, *B. menziesii* and *Xylomelum angustifolium* (Proteaceae), and *Eucalyptus todtiana* (Myrtaceae). Individuals of *B. menziesii*, *X. angustifolium* and *E. todtiana* can achieve tree size (3–5 m tall) and emerge above the general shrub layer while *B. attenuata*, *B. menziesii* and *B. hookeriana* dominate the shrub layer (1–2 m). The study species vary in their responses to fire, flowering phenology, and fecundity (Enright & Lamont 1989, 1992) but they are all confined to deep sands, have the highest leaf area index and the deepest and widest root systems of species in the community, enabling them to access subsurface-stored water and thus transpire and grow throughout the summer-autumn drought (Lamont & Bergl 1991; Pate & Bell 1999). They have large winged seeds (except for *E. todtiana*), which are released from woody fruits after fire. Their seedlings grow fast and develop a long taproot early (Enright & Lamont 1992; Milberg & Lamont 1997; Schütz *et al.* 2002), so that throughout their life cycle these species are drought-avoiders rather than drought-tolerators. Many other species in the community are also serotinous, but generally are sub-shrubs, with smaller seeds held at lower heights and shallower root systems that cannot access sufficient soil water to keep transpiring over the summer (Lamont *et al.* 1993, Pate & Bell 1999; Enright *et al.*

2007). *Eucalyptus todtiana*, by far the largest species in the area, has a massive lignotuber, and has a major influence on the ecosystem where it occurs; a number of species are found only under its crown (N.J. Enright, unpublished data).

The entire area of each dune was searched for the occurrence of each of the functional group species. The number of plants for each of *B. attenuata* and *B. hookeriana* on each dune was determined for six randomly chosen 10 × 10 m plots, while for the other three (less abundant) species, five plots with a diameter of 100 m were surveyed to estimate densities on each dune. Populations on small dunes were determined by counting all individual plants of each target species directly. The number of *E. todtiana* patches was cross-checked on satellite images from Google Earth (<http://earth.google.com>). The area of each dune was calculated using ImageJ (available from <http://rsb.info.nih.gov/ij>) after adapting the image of dune distribution from Google Earth. Consequently, the size of larger populations of each species was determined from the average plant density in the plots and dune area, since none of the five species appeared patchily distributed within dunes. Dune heights were calculated by interpolating the local elevations of adjacent swales and crests from a digital map with 2 m contour intervals (Department of Environment and Conservation, Government of Western Australia, unpublished map).

Measures of species diversity, based on the five species noted above, were species richness (N_s) and evenness (E). N_s is the number of the possible five species occurring on each dune (community), and E is calculated using a version of Simpson's diversity index as $1/\sum f_i^2$, where f_i is the relative frequency of species i . Both measures of species diversity were calculated using PRIMER v5.0 (PRIMER-E Ltd. Plymouth, UK).

Genetic variation for populations of *B. attenuata* sampled from the same 27 dunes

was measured using 11 microsatellite DNA primers. The detailed protocol for microsatellite genotyping is described in He *et al.* (2007). Two parameters, allelic richness (N_a) and expected heterozygosity (H_e), which are analogous to N_s and E (Etienne 2005), were calculated by GenAlEx 6 (Peakall & Smouse 2006). To eliminate the effect of uneven sample size on the measurements of number of alleles per locus, a rarefaction procedure was implemented using HP-RARE 1.0 (Kalinowski 2005). The rarefaction procedure re-samples individuals from populations with sample size larger than the minimum to calculate allelic richness expected if the smallest samples were taken from each population (Gotelli & Colwell 2001).

STATISTICAL ANALYSIS

Dune area and population size were log transformed to meet normality requirements. The SGDC was tested by correlating N_s with its analogous N_a , and E with H_e , respectively, using general linear models. The total effects of habitat properties (dune height and dune area) were also individually correlated with the four diversity parameters of diversity (N_s , E , N_a and H_e) using general linear models. Stepwise multiple regressions were carried out to determine the relative contribution of dune properties and one level of diversity to variance of the other level of diversity. Path analysis was carried out to determine the possible pathways of effects between environmental properties (dune area and dune height), species diversity (N_s and E) and genetic diversity (N_a and H_e), and a best-fit reduced model was built to show the pathway of significant correlations. General linear regressions were conducted in STATISTICA (StatSoft Inc.) and path analysis was implemented in AMOS 7.0 (SPSS Inc., Chicago, IL). Statistical significance was taken at the level of $P < 0.05$.

Results

FIELD SURVEY

For the 27 surveyed sand dunes containing *B. attenuata*, dune area ranged from 1.5 ha to 54.3 ha (averaging 10 ha), while dune height ranged from 1 to 8 m with an average of 3.4 m (Table 1). The number of the five target species present on each dune ranged from one (only *B. attenuata*) to five, and population size of each species also varied greatly (Table 1). The population sizes of all five species were significantly correlated with each other (all $P_s < 0.001$) and the population size of all five species was positively correlated with dune height and dune area ($P_s < 0.01$). Species diversity of this functional group varied from dune to dune, in terms of species richness (N_s) and evenness index (E).

CORRELATIONS BETWEEN GENETIC DIVERSITY, SPECIES DIVERSITY AND DUNE DIMENSIONS

Genetic diversity in populations of *Banksia attenuata* was measured by microsatellite markers. The number of alleles per locus (N_a) per population after rarefaction ranged from 4.5 (BA27) to 6.3 (BA20), with an average of 5.8, while the mean expected heterozygosity (H_e) varied from 0.581 (BA27) to 0.778 in BA01 (Table 1). N_a was correlated with dune height ($R^2 = 0.310$, $P = 0.002$), but was unaffected by dune area ($R^2 = 0.113$, $P = 0.085$), while H_e was correlated with both dune area ($R^2 = 0.175$, $P = 0.029$) and dune height ($R^2 = 0.193$, $P = 0.022$). Stepwise multiple regression showed that N_a was a significant function of N_s but not of dune height or area.

Measures of genetic diversity for *B. attenuata* (N_a and H_e) were positively

correlated with functional group species diversity (N_s and E) (Fig. 1). Stepwise multiple regression showed that N_s was a significant function of dune height, but not of area or N_a . Path analysis revealed a network effect between dune dimensions (dune height, dune area), species diversity (N_s and E) and genetic diversity (N_a and H_e) (Fig. 2). Dune height had greater total effects on species diversity (N_s and E) and genetic diversity (N_a and H_e) than dune area (Table 2), suggesting that dune height is driving the positive SGDC. Dune height, rather than dune area, determined variation in N_s , while the effect of dune height on N_a was largely via its effect on N_s : the direct effect of dune height on N_a was 0.28 and non-significant, while the indirect effect (via N_s) was 0.50 and significant. E was largely a function of N_s and H_e essentially a function of N_a (Fig. 2), and both responded to dune dimensions independently (Table 2).

Discussion

COVARIATION BETWEEN SPECIES DIVERSITY AND GENETIC DIVERSITY

We demonstrate a positive covariation between species diversity of the large shrub-small tree functional group and the genetic diversity of its most consistent member, *Banksia attenuata*. Further, this covariation was shown to be driven by common habitat properties. These results provide rarely tested empirical support for the hypothesis that species diversity within communities and genetic diversity within associated populations in widely varying but common habitats covary positively (Cleary *et al.* 2006; Wehenkel *et al.* 2006). Even rarer are studies that also attempt to determine an environmental explanation for any covariation (Karlin *et al.* 1984; Vellend 2003, 2005; Vellend & Geber 2005).

Unlike Velland (2003) and subsequent papers that built on island biogeography theory, our results of possible environmental causes do not give a central place to

‘island’ (dune) area. Instead, correlations between species diversity of the plant functional group and genetic diversity of *Banksia attenuata* are the result of their common response to dune height, which is essentially an index of water availability. Dunes with deeper sands can store a greater volume of groundwater (Lamont *et al.* 1989; Enright & Lamont 1992), crucial for species survival during the hot, dry summers in this region.

Taller dunes are more likely to promote survival of all dune-restricted species, and therefore species diversity. Conversely, local extinction of some species, especially following unusually dry winters, decreases species diversity on the lower dunes, as shown by population extinction in *B. hookeriana* due to exceptional drought (T. He & B.B. Lamont, unpublished data). Lamont *et al.* (1989) demonstrated the death of high numbers of seedlings competing for water at drier sites independent of species composition, while on the sand dunes, density of seedlings was little affected by competition. Similarly, genetic diversity in *B. attenuata* populations was greater on the higher dunes because more individuals (total, and relative to seed supply), and thus more genotypes, can survive there. With the better growing conditions, individual plants are larger and more fecund, including greater percentage seed set, so that a greater range of genotypes can be present (Lamont *et al.* 1994, 2003).

Our study has also shown that species richness itself may have an important effect on the level of allelic richness in *Banksia attenuata* populations. Coexistence with other species may hold promise of better establishment and survival, and thus more alleles, of *B. attenuata* by providing shelter for seeds to avoid predation and for seedling establishment, e.g. litter patches after wildfire (Lamont *et al.* 1993). Moreover, the coexistence of populations of functionally related species may be crucial for the maintenance of pollinators and wide outcrossing promoting genetic

variation. Banksias in the study area flower out of phase and are pollinated mainly by nectar-feeding birds and small marsupials (Wiens *et al.* 1979; Whelan & Burbidge 1980; Lamont *et al.* 2003). The presence of *E. todtiana*, one of the few tree species in the region, may also provide shelter and nesting places for these birds, while other *Banksia* species provide food for the pollinators when *B. attenuata* is not flowering.

Microsatellite DNA variation is generally assumed to have a neutral effect on phenotype (Selkoe & Toonen 2006). The net biology of a species is considered equivalent in the neutral theory of community ecology (Hubbell 2001), which led Etienne & Olff (2004) to suggest that any positive correlation between genetic and species diversity may be interpreted as “evidence of neutral processes”, and “it provides a new test of the neutral model”. Vellend & Geber (2005) also suggested that the parallel action of neutral processes on the two levels of diversity is a likely explanation for positive species diversity–genetic diversity relationships. However, our analysis has revealed that covariation between these two components of diversity was driven by common habitat properties, rather than neutral processes. These results suggest that interactions between alleles and species within the shared physical environment are more important than neutral processes in this landscape.

Conclusions

Genetic diversity and species diversity are inseparable components of biodiversity. The present work revealed a positive covariation between genetic diversity within populations of *Banksia attenuata* and species diversity within a single plant functional group of which it is a member. These correlations are more likely to be the result of the parallel action of similar responses to common habitat conditions rather than the outcome of neutral processes. Establishing such a relationship provides the

opportunity to predict one level of diversity on the basis of the other, with implications for rationalizing biodiversity conservation, monitoring and research efforts.

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References

- Alonso, D., Etienne, P.S. & Mckane, A.J. (2006) The merits of neutral theory. *Trends in Ecology & Evolution*, **21**, 451-458.
- Antonovics, J. (1976) The input from population genetics: “the new ecological genetics”. *Systematic Botany*, **1**, 233-245.
- Antonovics, J. (2003) Toward community genetics? *Ecology*, **84**, 598-601.
- Bell, G. (2001) Neutral macroecology. *Science*, **293**, 2413-2418.
- Booth, R.E. & Grime, J.P. (2003) Effects of genetic impoverishment on plant community diversity. *Journal of Ecology*, **91**, 721-730.
- Calviño-Cancela, M., He, T. & Lamont, B.B. (2008) Distribution of myrmecochorous species over the landscape and their potential long-distance dispersal by emus and kangaroos. *Diversity & Distributions*, **14**, 11-17.
- Chave, J. (2004) Neutral theory and community ecology. *Ecology Letters*, **7**, 241-253.

- Cleary, D.F.R., Fauvelot, C., Genner, M.J., Menken, S.B.J. & Mooers, A.O. (2006) Parallel responses of species and genetic diversity to El Nino Southern Oscillation-induced environmental destruction. *Ecology Letters*, **9**, 301-307.
- Enright, N.J. & Lamont, B.B. (1989) Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *Journal of Ecology*, **77**, 1111-1122.
- Enright, N.J. & Lamont, B.B. (1992) Recruitment variability in the resprouting shrub *Banksia attenuata* and non-sprouting congeners in the northern sandplain heaths of south-western Australia. *Acta Oecologica*, **13**, 727-741.
- Enright, N.J., Mosner, E., Miller, B.P., Johnson, N. & Lamont B.B. (2007) Patterns of soil *versus* canopy seed storage and plant species coexistence in species-rich shrublands of southwestern Australia. *Ecology*, **88**, 2292-2304.
- Etienne, R.S. (2005) A New sampling formula for neutral biodiversity. *Ecology letters*, **8**, 253-260.
- Etienne, R.S., Olff, H. (2004) A novel genealogical approach to neutral biodiversity theory. *Ecology Letters*, **7**, 170-175.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison species richness. *Ecology Letters*, **4**, 379-391.
- He, T., Krauss, S.L., Lamont, B.B., Miller, B.P. & Enright, N.J. (2004) Long distance dispersal in a metapopulation of *Banksia hookeriana* inferred by population allocation from AFLP data. *Molecular Ecology*, **13**, 1099-1109.
- He, T., Krauss, S.L. & Lamont, B.B. (2007) Polymorphic microsatellite markers for *Banksia attenuata* (Proteaceae). *Molecular Ecology Notes*, **7**, 1329-1331.
- Hnatiuk, R.J. & Hopkins, A.J.M. (1981) An ecological analysis of kwongan

- vegetation south of Eneabba, Western Australia. *Australian Journal of Ecology*, **6**, 423-438.
- Hopper, S.D. & Gioia, P. (2004) The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Reviews of Ecology, Evolution & Systematics*, **35**, 623-650.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Kalionwski, S.T. (2005) HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes*, **5**, 187-189.
- Karlin, A.A., Guttman, S.I. & Rathbun, S.L. (1984) Spatial autocorrelation analysis of heterozygosity and geograph distribution in populations of *Desmognathus fuscus* (Amphibia, Plethodontidae). *Copeia*, **2**, 343-356.
- Lamont, B.B. & Bergl, S.M. (1991) Water relations, shoot and root architecture, and phenology of three co-occurring *Banksia* species: no evidence for niche differentiation in the pattern of water use. *Oikos*, **60**, 291-298.
- Lamont, B.B., Enright, N.J. & Bergl, S.M. (1989) Coexistence and competitive exclusion of *Banksia hookeriana* in the presence of congeneric seedlings along a topographic gradient. *Oikos*, **56**, 39-42.
- Lamont, B.B., He, T., Enright, N.J., Krauss, S.L. & Miller, B.P. 2003. Anthropogenic disturbance promotes hybridization between *Banksia* species by altering their biology. *Journal of Evolutionary Biology*, **16**, 551-557.
- Lamont, B.B., Rees, R., Witkowski, E.T. & Whitten, V. (1994) Comparative size, fecundity and ecophysiology of roadside plants of *Banksia hookeriana*. *Journal of Applied Ecology*, **31**, 137-144.

- Lamont, B.B., Witkowski, E.T.F. & Enright, N.J. (1993). Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology*, **74**, 501-512.
- Milberg, P. & Lamont, B.B. (1997) Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytologist*, **136**, 665-672.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 803-808.
- Pate, J.S. & Bell, T.L. (1999) Application of the ecosystem mimic concept to the species-rich Banksia woodlands of Western Australia. *Agroforestry Systems*, **45**, 303-341.
- Peakall, R. & Smouse, P.E. (2006) GenAlEx 6: genetic analysis in excel: Population genetic software for teaching and research. *Mol. Ecol. Notes*, **6**, 288-295
- Ricklefs, R.E. & Schluter, D. (1993). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press. Chicago.
- Schütz, W., Milberg, M. & Lamont, B.B. (2002) Germination requirements and seedling responses to water availability and soil type in four eucalypt species. *Acta Oecologia*, **23**, 23-30.
- Selkoe, K.A. & Toonen, R.J. (2006) Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecology Letters*, **9**, 615–629.
- Symstad, A.J. (2000) A test of the effects of functional group richness and composition on grassland invasibility. *Ecology*, **81**, 99-109.
- Vellend, M. (2003) Island biogeography of genes and species. *American Naturalist*, **162**, 358-365.
- Vellend, M. (2005) Species diversity and genetic diversity: parallel process and

- correlated patterns. *American Naturalist*, **166**, 199-215.
- Vellend, M. & Geber M.A. (2005) Connections between species diversity and genetic diversity. *Ecology Letters*, **8**, 767-781.
- Wehenkel, C., Bergmann, F. & Gregorius H. (2006) Is there a trade-off between species diversity and genetic diversity in forest tree communities? *Plant Ecology*, **185**, 151-161.
- Weins, D., Renfree, M. & Wooller, R.O. (1979) Pollen loads of honey possums (*Taripes spenserae*) and nonflying mammal pollination in Southwestern Australia. *Annals of the Missouri Botanical Garden*, **66**, 830-838.
- Whelan, R.J. & Burbidge, A.H. (1980) Flowering phenology, seed set and bird pollination of five Western Australian *Banksia* species. *Austral Ecology*, **5**, 1-7.

1 Table 1. Summary of demography and genetic diversity of the 27 studied populations of
2 *Banksia attenuata* and four other large shrub–small tree species, and species diversity
3 measures for the five species plant functional group per dune. Population size of *B.*
4 *attenuata* (BA), *B. hookeriana* (BH), *B. menziesii* (BM),, *Eucalyptus todtiana* (ET), and
5 *Xylomelum angustifolium* (XA); D_a : dune area; D_h : dune height; N_a : number of alleles
6 per locus, rarefacted to the smallest sample size; H_e , expected heterozygosity; N_s ,
7 number of species; E , evenness.

| Code | D_a (ha) | D_h (m) | S | N_a | H_e | BA | BH | BM | XA | ET | N_s | E |
|------|------------|-----------|-----|-------|-------|-------|-------|------|-----|-----|-------|-------|
| BA01 | 22.4 | 4 | 35 | 6.1 | 0.778 | 2900 | 5000 | 500 | 142 | 190 | 5 | 0.558 |
| BA02 | 54.3 | 7 | 36 | 5.9 | 0.738 | 12000 | 10000 | 1100 | 830 | 430 | 5 | 0.585 |
| BA03 | 20.7 | 5 | 35 | 5.9 | 0.761 | 3300 | 30 | 900 | 920 | 170 | 5 | 0.556 |
| BA04 | 3.7 | 1 | 31 | 5.6 | 0.725 | 200 | 0 | 0 | 0 | 12 | 2 | 0.107 |
| BA05 | 4.7 | 3 | 33 | 5.7 | 0.710 | 2100 | 100 | 40 | 15 | 50 | 5 | 0.167 |
| BA06 | 8.4 | 4 | 32 | 6.0 | 0.755 | 28000 | 5000 | 150 | 119 | 90 | 5 | 0.273 |
| BA07 | 10.0 | 5 | 35 | 5.8 | 0.735 | 6600 | 4000 | 300 | 124 | 80 | 5 | 0.516 |
| BA08 | 1.5 | 2 | 11 | 5.8 | 0.729 | 15 | 0 | 0 | 0 | 0 | 1 | 0.000 |
| BA09 | 5.0 | 5 | 34 | 6.1 | 0.751 | 1300 | 700 | 45 | 178 | 65 | 5 | 0.576 |
| BA10 | 10.6 | 5 | 35 | 5.9 | 0.742 | 2900 | 30 | 0 | 25 | 120 | 4 | 0.109 |
| BA11 | 2.9 | 5 | 31 | 6.3 | 0.763 | 400 | 200 | 5 | 23 | 40 | 5 | 0.547 |
| BA12 | 8.5 | 5 | 35 | 5.8 | 0.746 | 2700 | 20 | 10 | 0 | 35 | 4 | 0.046 |
| BA13 | 3.6 | 3 | 27 | 6.1 | 0.759 | 100 | 0 | 0 | 0 | 13 | 2 | 0.204 |
| BA14 | 8.3 | 2 | 34 | 5.9 | 0.752 | 1800 | 3 | 0 | 30 | 65 | 4 | 0.097 |
| BA15 | 14.1 | 6 | 32 | 5.9 | 0.739 | 1800 | 400 | 15 | 556 | 125 | 5 | 0.556 |
| BA16 | 1.9 | 3 | 13 | 5.8 | 0.716 | 40 | 0 | 2 | 0 | 25 | 3 | 0.504 |
| BA17 | 15.5 | 3 | 30 | 6.0 | 0.738 | 1700 | 2000 | 20 | 276 | 195 | 5 | 0.601 |
| BA18 | 7.9 | 3 | 32 | 6.1 | 0.761 | 900 | 790 | 10 | 228 | 100 | 5 | 0.636 |
| BA19 | 18.0 | 4 | 32 | 5.7 | 0.726 | 2000 | 1800 | 10 | 825 | 325 | 5 | 0.674 |
| BA20 | 15.8 | 8 | 34 | 6.2 | 0.763 | 4700 | 800 | 150 | 905 | 170 | 5 | 0.478 |
| BA21 | 12.8 | 2 | 25 | 5.8 | 0.736 | 1600 | 0 | 0 | 0 | 40 | 2 | 0.048 |
| BA22 | 7.0 | 1 | 22 | 5.7 | 0.748 | 740 | 0 | 0 | 0 | 30 | 2 | 0.075 |
| BA23 | 2.3 | 2 | 20 | 5.7 | 0.745 | 100 | 0 | 0 | 16 | 30 | 3 | 0.477 |
| BA24 | 2.2 | 1 | 20 | 5.7 | 0.720 | 1000 | 0 | 0 | 0 | 15 | 2 | 0.227 |
| BA25 | 8.3 | 1 | 10 | 5.2 | 0.695 | 12 | 0 | 0 | 0 | 3 | 2 | 0.320 |
| BA26 | 3.9 | 1 | 15 | 5.7 | 0.725 | 40 | 0 | 0 | 0 | 20 | 2 | 0.444 |
| BA27 | 1.6 | 1 | 7 | 4.5 | 0.581 | 11 | 0 | 0 | 0 | 0 | 1 | 0.000 |

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Table 2 Standardized effects of dune height and dune area on species diversity and genetic diversity calculated from the saturated path model. *, $P < 0.05$

| | | N_s | E | N_a | H_e |
|-------------|---------------|-------|-------|-------|--------|
| Dune height | Total effects | 0.78* | 0.50* | 0.58* | 0.44* |
| | Direct effect | 0.61* | -0.05 | 0.28 | -0.29* |
| Dune area | Total effects | 0.28* | 0.19* | -0.01 | 0.25* |
| | Direct effect | 0.28* | -0.01 | -0.15 | 0.26* |

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2 Figure captions

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4 Fig. 1 Plots of the relationship between functional group species diversity (species
5 richness N_s and evenness E) and genetic diversity of *B. attenuata* (rarefied allelic
6 richness N_a and heterozygosity H_e) (all $P < 0.05$).

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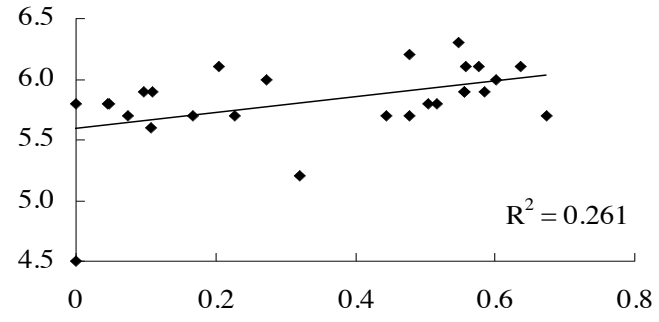
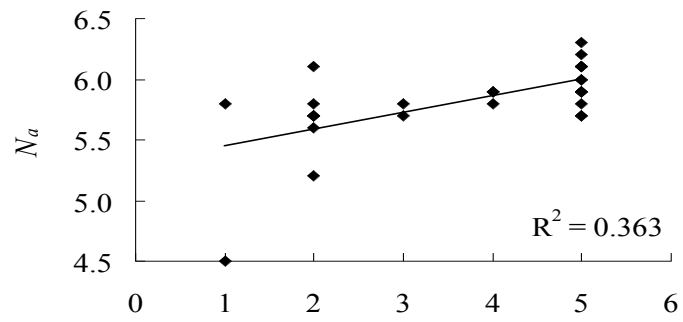
8 Fig. 2 Diagram showing the pathway of significant effects ($P < 0.05$) of dune
9 dimensions on species diversity and genetic diversity. Numbers show standardised direct
10 effects calculated from a reduced path model.

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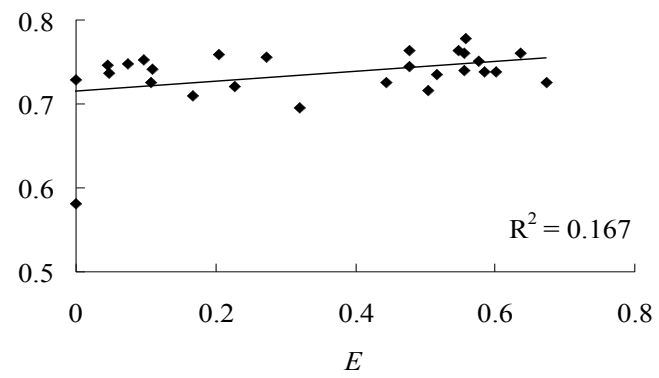
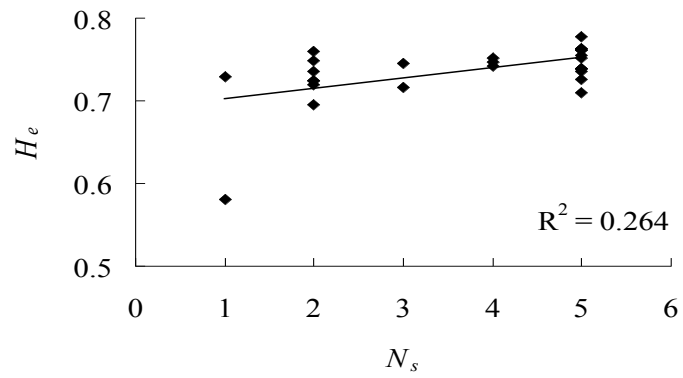
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1 Fig. 1



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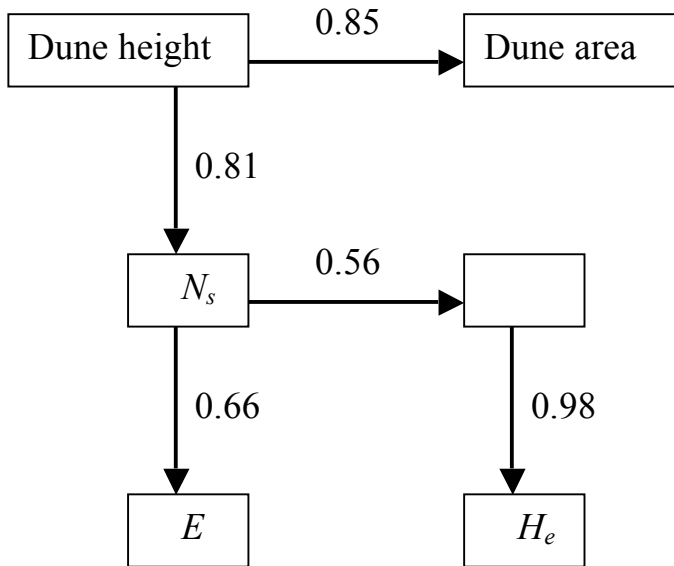


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2 Fig. 2

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