



Dispersal, edaphic fidelity and speciation in species-rich Western Australian shrublands: evaluating a neutral model of biodiversity

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Over evolutionary time, the number of species in a community reflects the balance between the rate of speciation and the rate of extinction. Over shorter time-scales local species richness is also affected by how often species move into and out of the local community. These processes are at the heart of Hubbell's 'unified neutral theory of biodiversity' (Hubbell 2001). Hubbell's spatially implicit, dispersal-limited neutral model is the most widely used of the many implementations of neutral theory and it provides an estimate of the rate of speciation in a metacommunity (if metacommunity size is known) and the rate at which species migrate into the local community from the wider metacommunity. Recently, this neutral model has been used to compare rates of speciation and migration in the species-rich fynbos of South Africa and in neotropical forests. Here we use new analytical methods for estimating the neutral model's parameters to infer speciation and dispersal rates for three sites in species-rich sclerophyll shrublands (equivalent to fynbos) in Western Australia (WA). Our estimates suggest that WA shrublands are intermediate between fynbos and tropical rainforest in terms of speciation and dispersal. Although a weak test, the model predicts species abundance distributions and species accumulation curves similar to those observed at the three sites. The neutral model's predictions also remain plausible when confronted with independent data describing: (1) known edaphic relationships between sites, (2) estimates of metacommunity species richness and (3) rates of speciation among resprouters and nonsprouters. Two of the site pairs, however, show species turnovers significantly different from those predicted by the spatially implicit form of the neutral model that we use. This suggests that non-neutral processes, in this case probably edaphic specialisation, are important in the WA shrubland metacommunity. The neutral model predicts similar rates of speciation in resprouter and sprouter taxa, a finding supported by recent molecular phylogenies. Finally, when converted into temporally scaled speciation rates and species longevity, the estimates produced by the neutral model seem implausible. The apparent departure from neutrality in the turnover of species between some sites and the implausible temporal dynamics may be due to the particular model chosen and does not reduce the significance of our other results, which confirm that local dispersal limitation, coupled with broader scale edaphic fidelity, combine to structure this biodiverse metacommunity.

The species richness of a community reflects a long-term balance between the rates at which speciation and extinction occur, mediated over shorter time-scales by the rate at which species migrate into and out of it. Hubbell (2001) developed a suite of neutral models that describe how the processes of speciation and migration might result in observed patterns of species richness via ecological drift, but numerous other neutral models have also been proposed (Caswell 1976, Chave 2004, Volkov et al. 2005, Etienne et al. 2007, Haegeman and Etienne 2008, Rosindell et al. 2008). What all neutral models have in common is that individuals interact in the same way with conspecifics and heterospecifics (the neutrality assumption). Together, such neutral models comprise a neutral theory of the dynamics of ecological communities.

Neutral model mechanics

Hubbell's most widely used neutral model is hierarchical in that it considers a regional metacommunity (a set of local communities linked by dispersal, Leibold, et al. 2004) comprised of J_M individuals, in which speciation occurs at rate v (speciation per individual per time-step), linked by migration, at rate m , to local communities containing J_L individuals. On their death, individuals in the local community are replaced either by an individual of a species currently present in the local community or by an immigrant species from the metacommunity. The probability of a given species i in the local community being replaced on its death by species j is proportional to the abundance of species j within the local community, or, in

the case of immigration, within the metacommunity. This process is termed ‘ecological drift’.

Metacommunity dynamics reflect speciation and extinction processes (Hubbell 2001). While three modes of speciation are possible in Hubbell’s neutral model, analytical solutions are currently available for only one, random point mutation (Hubbell 2001, 2003). Under random point mutation new species appear, at rate v , with an abundance of exactly one. Etienne and Alonso (2007) note that this is somewhat analogous to polyploidy in plants and Ricklefs (2003) points out that it would result in many cryptic species of low abundance: whether these species would be recognised as such in the field or by taxonomists is a moot point. The other two speciation models are random fission and peripheral isolate speciation; the former is analogous to allopatric speciation and the latter considers speciation in spatially fragmented populations (Chave 2004). Chave and Leigh (2002) and Zillio and Condit (2007) argue that speciation in neutral models should not be interpreted as the ‘birth of new species’ in the strict genetic sense, but rather as species origination, which includes both true speciation and the long-distance dispersal of novel species into the metacommunity.

Independent of how speciation is represented, there are at least two forms of the neutral model with respect to temporal dynamics (Etienne and Alonso 2007). Individuals in the metacommunity die at each discrete time step such that the time-steps of models may represent either: (1) all individuals reproducing and dying with non-overlapping generations (the Wright–Fisher model), or (2) the reproduction and death of single individuals with overlapping generations (the Moran model). Although using some equations from the Wright–Fisher model, Hubbell (2001) described the neutral model in terms of the Moran model, but with a subtle difference: while individuals that die in the Moran model still contribute to the pool of recruits, in the Hubbell model they do not (Etienne et al. 2007). Importantly, all three forms of the model yield the same equilibrium conditions (assuming the speciation rate is very low) but differ in the time scale of their dynamics (Blythe and McKane 2007, Etienne and Alonso 2007).

The two key parameters in Hubbell’s neutral model are the ‘fundamental biodiversity number’, θ (Hubbell 2001), and the ‘fundamental dispersal number’, I (Etienne and Alonso 2005). θ indexes the process of speciation in the metacommunity:

$$\theta = 2J_e u \quad (1)$$

where: u = speciation rate (per generation) and J_e is the effective metacommunity size (the metacommunity size rescaled to ensure the dynamics of different versions of neutral models are consistent – Etienne and Alonso 2007).

θ can be used to make quantitative predictions about the number of species and their lifespan in the metacommunity that are testable with independent data. We will explicitly state some of these predictions here, as we use them in our analyses.

1. The expected number of species ($E[S, \theta]$) in the metacommunity, for speciation via point mutation is (Vallade and Houchmandzadeh 2003, Etienne and Olff 2004):

$$E[S, \theta] = \sum_{i=1}^{J_M} \frac{\theta}{\theta + i - 1} = \theta(\Psi(\theta + J_M) - \Psi(\theta)) \quad (2)$$

where: $\Psi(x)$ is the Psi or digamma function.

2. The average lifespan (time to extinction from an abundance of one) for a given species (number of generations), under point mutation is:

$$\text{species longevity} = \frac{E[S, \theta]}{J_M \times u} \quad (3)$$

3. Under pure ecological drift, the age in generations (A) of a species starting with abundance x_0 ($x_0 = 1$ under point mutation) and current abundance x is approximately (Etienne et al. 2007b):

$$A(x, x_0) \approx -2J_M \left[\frac{x}{1-x} \log(x) \right] \text{ assuming } x_0 \ll x \quad (4)$$

The second key parameter, m , describes the rate of migration from the metacommunity to a single local community ($0 \leq m \leq 1$); m is the probability that a dying individual is replaced by an individual from a species from the wider metacommunity. Low values of m suggest that the local community receives few immigrants from the wider metacommunity and so it is ‘dispersal limited’, while $m = 1$ indicates no dispersal limitation. Because m is affected by the number of individuals in the local community (J_L), I is used when data are combined from multiple samples across the metacommunity (Etienne 2007, as $m \rightarrow 1$, $I \rightarrow \infty$):

$$I = \frac{m}{(1-m)} \times (J_L - 1) \quad (5)$$

where: J_L is the local community size (usually assumed to be the same as the sample size, J).

I can be interpreted as the number of individuals in the metacommunity competing for a site in the local community (Etienne and Olff 2004), and it provides a measure of recruitment limitation, encompassing both dispersal and establishment limitation, relative to resident individuals (Jabot et al. 2008). It is perhaps therefore better called the ‘fundamental immigration number’ (Munoz et al. 2007).

Evaluating Hubbell’s neutral model

Neutral theory remains much debated on both conceptual and empirical grounds (Chave 2004, Alonso et al. 2006, Holyoak and Loreau 2006, McGill et al. 2006, Leigh 2007). In particular the assumption of equivalence between trophically-similar species has been strongly contested. Nevertheless, neutral models offer a simple representation of biological systems and their parameters are biologically interpretable. Thus, they can act as a quantitative null model with which to confront observed community patterns (Maurer and McGill 2004, Hubbell 2006, Leigh 2007, Zillio and Condit 2007). Even if their assumptions seem biologically untenable, neutral models still represent a valid approach to the question of how much of a community’s structure can be explained on the basis of ecological drift and dispersal limitation alone (Hubbell

2006). And, this question of understanding the relative roles of dispersal limitation and local environmental filtering is central to understanding the fundamental ecological problem of explaining spatial variation in species abundances (Cottenie 2005, Jabot et al. 2008).

The standard empirical evaluation of neutral theory has involved the comparison of predicted and observed species abundance distributions (McGill et al. 2006, Leigh 2007). However, comparison of a model to data via curve-fitting provides a weak evaluation of any model (McGill 2003), not least because many models may equally explain a body of observations (Oreskes et al. 1994). Indeed, both Purves and Pacala (2005) and Walker (2007) demonstrate how apparently neutral patterns can result from non-neutral dynamics. However, estimates from fitted neutral models do (1) allow testing of independent predictions to assess how well the model applies and where it fails, and (2) provide broad insight into the forces driving and maintaining species richness. Latimer et al. (2005) and Etienne et al. (2006) used neutral model parameter estimates to compare rates of speciation and migration of plant species in contrasting species-rich systems and to compare these estimates with their ecological understanding of these systems. They showed that the species-rich Mediterranean-type shrubland (fynbos) communities of the Cape Floristic Region are typified by high levels of local speciation and low levels of migration, while tropical rainforests tended to show the opposite pattern. Latimer et al. (2005) concluded that the fynbos has arrived at high species-richness by a different route than the tropical rainforests of Central and South America. Their analyses suggested that while local speciation was comparatively uncommon in the tropical rainforests communities they studied, migration rates were high (i.e. low θ –high m) and that, conversely, speciation was frequent in the fynbos, but migration rates were low (i.e. high θ –low m).

Here we use recently developed analytical methods that allow exact solution of the dispersal-limited neutral theory (Etienne 2005, 2007, 2009a, Munoz et al. 2007) to quantify speciation and migration rates in species-rich Mediterranean-type shrubland (kwongan) communities of the Southwest Floristic Region of Western Australia (Hopper and Gioia 2004). We compare the predictions of the neutral model with independent estimates of these values. These kwongan communities are ecological analogues (Cowling et al. 1996) to the fynbos shrublands considered by Latimer et al. (2005). In particular, we sought to:

1. Determine the similarities and differences between the estimated rates of speciation and migration for the species-rich kwongan of the Southwest Floristic Region, and the fynbos and tropical rainforest communities reported by Latimer et al. (2005) and others,
2. Evaluate the extent to which estimates of θ , based on multiple sites, recover the known edaphic and ecological similarities between individual pairs of sites, and the extent to which I captures likely differences in establishment difficulty between the three sites,
3. Evaluate the plausibility of the metacommunity species richness, speciation and species longevity

estimates produced by Hubbell's neutral model under point mutation speciation (the only speciation model for which analytical solutions are currently available),

4. Compare rates of speciation in resprouter and perennial nonsprouter species as predicted by the neutral model with recent molecular phylogenies that compare the two groups (Verdú et al. 2007).

Methods

Study area and flora

The Mediterranean-type flora of southwestern Australia is a recognised biodiversity hotspot (Cowling et al. 1996, Myers et al. 2000, Hopper and Gioia 2004). The Southwest Floristic Region covers an area of 302 000 km² and contains 7380 species and sub-species of which at least 60% are endemic to the region (Hopper and Gioia 2004). Similar to the Mediterranean-type Cape Floristic Region, the Southwest Floristic Region harbours many recognised 'species flocks' (i.e. highly speciose genera – Cowling et al. 1996, Cowling and Lamont 1998), and speciation rates in both regions are believed to be exceptionally high. Cowling et al. (1996) argue that much of the speciation in these systems is edaphically driven (Hopper 1979). Cowling et al. (1996) also note that the fynbos and kwongan might have high speciation and relatively low rates of extinction due to (1) the high fire frequencies they experience, and (2) their relatively mild climates during the glacial–interglacial cycles of the Quaternary Period.

There are two fundamentally different life-history syndromes in the sclerophyll shrublands that we consider: species killed by fire (nonsprouters, with discrete generations) and those that resprout after fire (resprouters, with overlapping generations). Resprouters have an individual longevity of 150–300 years or more (as high as 1000 years in some species). The maximum longevity of individual nonsprouters is approximately 60 years, although their lifespan is controlled by the fire regime which is generally shorter, with current return interval of about 13 years (Lamont and Wiens 2003, Miller et al. 2007), so that potential longevity is rarely reached. Thus, we assume generation lengths of 13 years for nonsprouters and 150–300 years for resprouters. Given the shorter and discrete generations of nonsprouters it might be expected that their speciation rates are faster than resprouters. However, recent molecular phylogenies (Verdú et al. 2007) and frequency analyses (Lamont and Wiens 2003) suggest, surprisingly, that the two groups have similar rates of speciation and diversification.

Data collection

We collected data from three species-rich kwongan communities on low-nutrient, acid sandplains near Eneabba, 275 km north of Perth, WA (Fig. 1). The Eneabba Plain encompasses an area of 700 km² (Miller et al. 2007), and harbours about 1100 vascular plant species (a likely underestimate given the current rate of description of new taxa in SW WA). The three sample plots (one of 40 × 40 m and two of 30 × 30 m) each contained at least 10 000

individuals and up to 113 species (196 species in total across the three plots); Chiarucci et al. (2003) and Enright et al. (2007) provide full details of the sites and their sampling. Sites were located in (1) a tall shrubland on deep acid sands of a low dune (Crest), (2) a low shrubland on shallow acid sands overlying crests of an inter-dune (Swale), and (3) a low shrubland on shallow sands overlying lateritic gravels (Laterite), to provide three high-diversity data sets spanning a range of substrates. The Crest and Swale sites were separated by less than 1 km and the Crest and Laterite and Swale and Laterite were about 30 km from each other (Fig. 1). Although there are edaphic and compositional differences between the three sample sites they share a number of species (10–42% similarity, Sørensen's index) and so are not floristically discrete. The sites were last burned at least 12 years prior to mapping, and represented mature phase vegetation. Based on the soil nutrient levels, water availability and post-fire productivity, resource availability at the three sites can be ordered as Crest > Laterite ≈ Swale (Perry et al. 2008).

On the basis of its floristic composition and geology we consider the Eneabba Plain to be a single system (metacommunity) with local differences in species composition and structure related to substrate variation as described

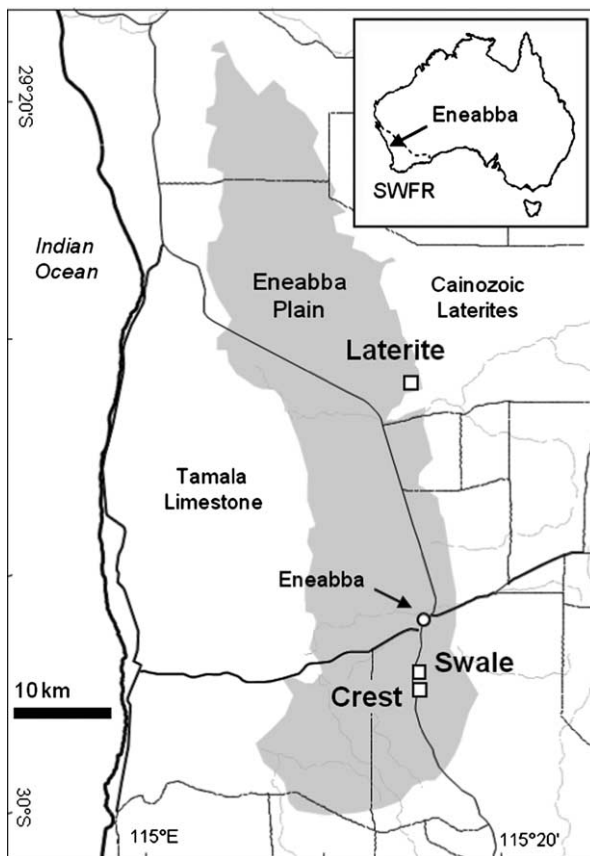


Figure 1. Regional setting of the three datasets analysed here; the grey-shaded area is the extent of the Eneabba Plain. The location of Eneabba township 275 km north of Perth is broadly indicated in the inset map of Australia which also shows the extent of the SW Floristic Region. Note that the Crest and Swale sites are close together (<1 km) and are equidistant (30 km) from the Laterite site.

above. Nevertheless, while clearly differentiated from surrounding vegetation on other geologies, the sandplain metacommunity is not closed to species immigration. Extant compositional similarity with nearby calcareous shrublands is around 20% (Enright et al. 2007), and repeated migrations of species across the sandplain are likely to have occurred in response to the climate oscillations of the Quaternary Period (Hopper and Gioia 2004). Based on stem densities at the three sites, and the area of the Eneabba Plain, we estimate the metacommunity size (J_M) as between 0.5×10^{10} and 1.1×10^{10} individuals. Combining the stem density across all three sites gives an intermediate estimate of metacommunity size of 7.7×10^9 individuals ($10.88 \text{ stems m}^{-2}$ [$37\,008$ individuals in 3400 m^2], distributed across 707 km^2).

Estimating neutral model parameters

We aggregated the data across the three sites to form (1) a single 'combined' sample, and (2) three samples of pairs of 'combined' sites (i.e. Crest and Laterite, Crest and Swale, Laterite and Swale). By 'combined' we mean that the multi-site samples maintain their site identities. We did not lump (i.e. pool without maintaining site identities) the three local samples, because the plots were separated by distances greater than the mean dispersal distance (Etienne 2007, Munoz et al. 2007). With the assumption that speciation follows the point mutation model, Etienne's (2007) sampling formula provides the probability of observing the vector of species' abundances (\mathbf{n}) given θ , the I values for each site, summarized in the vector $\mathbf{I} = (I_1, I_2, I_3)$, and the sample sizes summarized in the vector $\mathbf{J} = (J_1, J_2, J_3)$ (i.e. $P[\mathbf{n}|\theta, \mathbf{I}, \mathbf{J}]$). This formula, which is a generalisation for multiple, spatially separated samples of the single-sample result (Etienne 2005), can be used to obtain maximum likelihood estimates of the model parameters. While Etienne (2007) states that the I-values must be identical for all sites to be able to obtain parameter estimates in practice, we used a recent generalisation of this formula where this assumption is not necessary (Etienne 2009b). We also divided each sample into nonsprouter and sprouter species and estimated θ and I-values for both. The algorithm that maximises the joint likelihood for all parameters simultaneously is computationally demanding. Therefore, we used starting values for this algorithm obtained from the approximate approach of Etienne (2009a). We also specified estimates of the errors in the parameters based on the observed information matrix at the likelihood optimum (Etienne 2009b).

Model comparison and evaluation

While curve-fitting is problematic for model evaluation (McGill 2003, McGill et al. 2006), it is useful for assessing the degree to which a model can recover the data used to parameterise it. Hubbell's neutral model has failed this test in some cases (Walker and Cyr 2007). Our first evaluation of the model is a curve-fitting assessment of the species abundance distributions for the Eneabba Plain communities and a comparison of our estimates of θ and I with those from comparably species-rich plant communities. Demon-

strating departure from neutrality (i.e. rejecting null hypotheses provided by the neutral model) is a useful first step in developing explanations for community structure and organisation (Leigh 2007). We use the ‘exact’ test of neutrality described by (Etienne 2007) to assess the extent to which the Eneabba Plain communities and metacommunity may deviate from neutrality. This method involves constructing many artificial neutral communities using the sample size vector **J** and the MLE estimates of θ and **I** from the observed data. To evaluate any departure from neutrality we compare statistics from the real communities with the frequency distribution of the same statistic from the artificial datasets. We use two measures: (1) the log-likelihood of the vector of species abundances (**n**) given θ , **I** and **J**, and (2) the dissimilarity between site pairs (based on Sørensen’s index). Use of the log-likelihood allows us to assess the extent to which the neutral model we use can mimic the observed data, while use of the dissimilarity measure allows us to assess whether turnover between communities departs from that expected under neutrality. The significance of any departure from neutrality is assessed on the basis of the position of the observed statistic relative to the frequency distribution of simulated statistics. It is worth noting that in a strict sense any departure from neutrality applies only to the specific form of the neutral model used to make parameter estimates (in our case a spatially implicit form with speciation via point mutation).

A more rigorous approach to model evaluation is to confront a model’s predictions against independent data, and so we evaluate three of the neutral model’s predictions against (1) the nature of edaphic and ecological relationships between sites based on pairwise and three site estimates of θ , (2) estimates of metacommunity species

richness, speciation rates and species longevities, and (3) relative rates of speciation in resprouters and nonsprouters (Table 1). Because these predictions can be compared with estimates derived using other methods, such a comparison represents an independent test of the neutral model. Again, it is worth noting that neutral models have not always passed similar tests in other communities, with predictions of the rate of the metacommunity dynamics being particularly problematic (Nee 2005, Ricklefs 2006).

Parameter estimates from multiple local communities in the same metacommunity are potentially informative for evaluating the ecological meaning of the neutral model’s estimates (Etienne 2007, Munoz et al. 2007, Jabot et al. 2008). Under dispersal limitation (i.e. low *m*), θ will tend to be higher when estimated from multiple samples because those samples will tend to have relatively few species in common as compared with the case where local samples are simply random sub-samples of the metacommunity. Comparing estimates of θ from data combined across a network of *n* local communities (sites) with all possible site-pair estimates facilitates exploration of the importance of dispersal limitation and habitat variability. In a perfectly homogeneous system with no distance decay, the θ estimate for pairs of sites should be the same as for *n* sites. If distance decay (dispersal limitation) is structuring the metacommunity, there should be little difference in the θ -values estimated from multiple equidistant pairs of sites; if there is, this suggests that factors beyond dispersal limitation are important. In our case – where two of the three pairs are equidistant (Crest–Laterite and Laterite–Swale) and one pair is much closer together (Crest–Swale) – we would expect the equidistant pairs to have similar θ values. A difference in estimates of **I** between sites means that they

Table 1. Evaluations of the neutral model based on confronting predictions of site similarity in model parameters (θ and **I** estimated via maximum likelihood estimation [MLE]), metacommunity characteristics and speciation rates for the nonsprouter and resprouter components of the metacommunity.

Question	Method	Evaluation
1	Construct species abundance distributions with and without dispersal limitation using the estimates of θ and I (following Etienne 2005, Etienne 2007) Construct species accumulation curves with and without dispersal limitation using the estimates of θ and I (following Etienne and Olff 2004, Walker and Cyr 2007)	Compare observed parameter values with previously published values from similarly species-rich communities.
2	Comparison of pairwise estimates of θ and I with the three-site ‘mean’ for θ and I	θ for pairs of sites equal distances apart should be similar under dispersal limitation if distance-decay drives species turnover between sites. Evaluate the plausibility of our estimates of I against previously published information concerning long-distance seed dispersal (He et al. 2004, 2009a, 2009b) and edaphic fidelity/specialisation on the sandplain.
3	Estimate metacommunity richness ($E[S, \theta]$), speciation rates (<i>v</i>) and species ages from estimates of θ	Species richness for the metacommunity can be independently estimated from herbarium records and other published data. Evaluate the plausibility of these estimates against the known geological and ecological history of the area. Compare the observed data with simulated neutral communities based on the same parameter estimates (the ‘exact’ test of Etienne 2007).
4	Estimate θ separately for the nonsprouter and resprouter components of the metacommunity. Use these θ values to yield estimate of $E[S, \theta]$ and <i>v</i> for nonsprouters and resprouters.	Compare $E[S, \theta]$ with data as for 3. Compare <i>v</i> for the nonsprouters and resprouters with recent frequency analyses (Lamont and Wiens 2003) and molecular phylogenies (Verdú et al. 2007).

differ in either (1) the ease with which they are reached by the dispersers (for example due to physical barriers), or (2) the relative success of dispersers versus residents in establishment (Jabot et al. 2008).

Results

How do neutral model estimates of θ and I from the Eneabba shrublands compare with those for other species-rich communities?

Our neutral model parameter estimates suggest a closed system with high rates of speciation (i.e. high θ and low I). Based on the combined data, we find a θ (the fundamental biodiversity number) value of 114 and I (the fundamental dispersal number) values of 33, 20 and 34, for the Crest, Laterite and Swale, respectively (Table 2). Our estimates of θ are comparable with those for some tropical rainforest and fynbos communities (Table 3). The estimates of I are also comparable with those of the Cape Floristic Region fynbos, and are two to three orders of magnitude smaller than those observed in some tropical rainforest communities (Etienne et al. 2006, Latimer et al. 2005). Estimates of θ and I are higher for resprouters than for nonsprouters for the combined data, although estimates for the nonsprouters are variable due to small sample size effects (Table 2).

The neutral model provides qualitatively reasonable approximations to the observed abundance data (species abundance distributions and accumulation curves) for the three local communities (Fig. 2). The simulated dispersal-limited neutral communities are close in structure to the observed species abundance distribution, with the observed species abundance distribution consistently falling within the 5th and 95th percentile of the simulations. The species-accumulation curves predicted by the dispersal-limited model are also within the observed percentile limits at Crest and Laterite, but are less satisfactory at Swale, where the richness of sample sizes with $J_L < 5000$ is significantly

under-predicted. Comparison of the log-likelihood of the observed data with those of simulated neutral communities, confirms that the neutral model that we use mimics the data well (Fig. 3a), with the observed data falling in the middle of the frequency distribution of simulated values. Qualitatively, the kwongan species abundance distributions appear more similar to those of the tropical rain forest: they show fewer very dominant and relatively more rare species than the Cape Floristic Region plots described by Latimer et al. (2005).

Do estimates of θ and I reflect known edaphic and ecological similarities between the sites?

Our three-site estimates of θ can be interpreted as a 'mean' value for the metacommunity. The combined sample estimate for θ is 114, and two of the three site pairs have θ values close to this value (Fig. 4). Crest and Swale, separated by a distance of only 500 m, have a dissimilarity of 58%, and a combined θ (71) lower than the mean. Swale and Laterite, while 30 km apart, are edaphically more similar in that they are both highly water-limited (shallow sands) and have a low productivity: they have a dissimilarity of 77% and a combined θ of 98. Crest and Laterite, also 30 km apart, have a combined θ of 320, are highly dissimilar (91%) and are edaphically quite different, with much lower water availability and site productivity at Laterite. Given the distances between the three site pairs we would expect θ to be similar for Crest–Laterite and Laterite–Swale. This is not the case, and instead we see that Laterite–Swale and Crest–Swale have similar θ values despite being separated by very different distances. This suggests that distance decay is smaller between Swale and Laterite than Crest and Laterite; this is likely a function of the edaphic differences between Crest and the other two sites. Estimates for the resprouter and nonsprouter components of the community show a similar trend with Crest–Swale and Laterite–Swale pairs having θ -values close to, but consistently lower than, the

Table 2. Parameter estimates for all species and for the resprouter and nonsprouter components of the community for the dispersal-limited neutral model using the improved one-stage methods of parameter estimation (Etienne 2009b); J_L is the number of individuals in the local sample and S the species richness, Cr, La and Sw refer to the Crest, Laterite and Swale sites, respectively, and where subscripted to I refer to the estimate of I for that site. Numbers in parentheses are the estimates of the error in the parameter values.

	Sample size and species richness		MLE parameters			
	J_L	S	θ	I_{Cr}	I_{La}	I_{Sw}
All species						
CR-LA-SW	(10530, 13663, 12815)	(113, 93, 104)	114 (13)	33 (4.0)	20 (2.3)	34 (4.4)
CR-LA	(10530, 13663)	(113, 93)	320 (41)	24 (2.8)	17 (2.0)	
CR-SW	(10530, 12815)	(113, 104)	71 (8.9)	53 (8.3)		47 (7.4)
LA-SW	(13663, 12815)	(93, 104)	98 (14)		24 (3.2)	34 (4.9)
Resprouters						
CR-LA-SW [R]	(7017, 11511, 10225)	(75, 81, 77)	81 (10)	21 (3.1)	19 (2.5)	25 (3.8)
CR-LA [R]	(7017, 11511)	(75, 81)	146 (28)	16 (2.3)	16 (2.2)	
CR-SW [R]	(7017, 10225)	(75, 77)	46 (6.7)	36 (6.6)		40 (7.6)
LA-SW [R]	(11511, 10225)	(81, 77)	77 (12)		22 (3.3)	24 (3.7)
Nonsprouters						
CR-LA-SW [N]	(3513, 2152, 2590)	(38, 12, 27)	30 (6.9)	13 (3.1)	1.9 (0.6)	8.6 (2.3)
CR-LA [N]	(3513, 2152)	(31, 12)	87 (41)	7.7 (1.7)	1.7 (0.5)	
CR-SW [N]	(3513, 2590)	(38, 27)	25 (6.2)	17 (5.1)		9.4 (2.7)
LA-SW [N]	(2152, 2590)	(12, 27)	17 (5.9)		2.3 (0.8)	12 (4.9)

Table 3. Range of estimates of θ and I for species-rich fynbos and tropical rainforest communities; parameter estimates are based on exact likelihood calculations (data from Latimer et al. 2005, Etienne et al. 2006, Etienne 2007). I values for the Panamanian forest plots are for single samples only. m values are not presented for the Panama data as they are not reported by Etienne (2007); values of ∞ for I suggest m values close to 1.

System	Species	Individuals	θ	m	I
Fynbos, South Africa	114–247	8 916–24 003	32–384	0.01–0.27	66–8 878
Tropical rainforests, Central America	225–648	7 613–21 457	48–187	0.09–0.53	2 200–7 612
Panamanian tropical rainforest plots	99–225	1 079–21 457	259	–	2 211– ∞

three-site ‘mean’, while that for the Crest–Laterite pair is markedly higher. Based on the exact test of neutrality (Fig. 3b–d), the Crest–Laterite pair is more dissimilar (observed = 91%, mean simulated = 82%; $p < 0.01$) than

the neutral model predicts, and the Crest–Swale pair less dissimilar (obs = 58%, mean sim. = 78%; $p < 0.001$). The Laterite–Swale pair is as dissimilar as we would expect under neutrality (obs = 77%, mean sim. = 81%; $p = 0.21$).

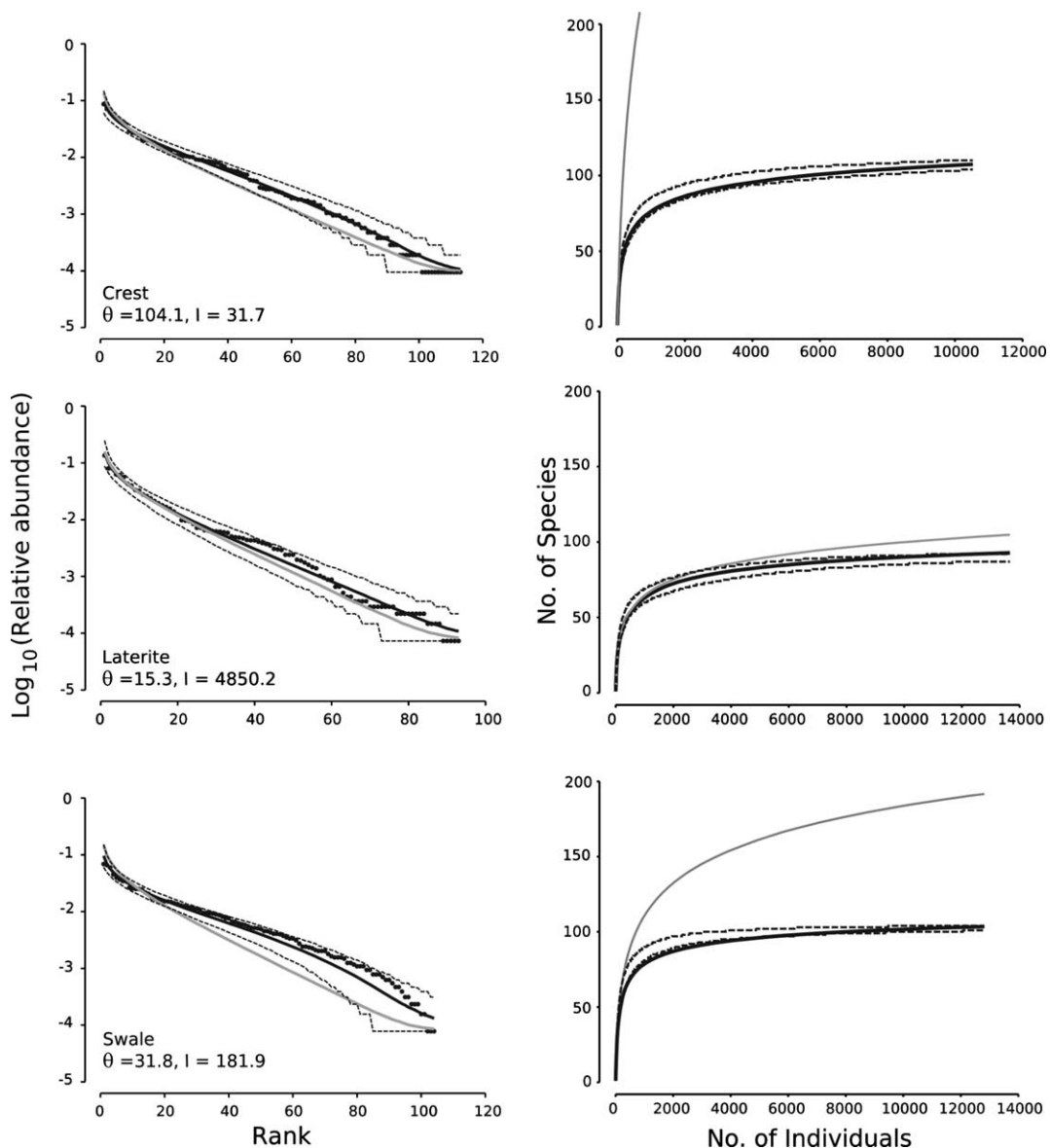


Figure 2. Rank–abundance distribution (left) and species accumulation curves (SAC, right) for the three sites showing the observed data (filled circles). The species abundance distribution curves show the average of 999 simulations of the dispersal limited (solid line) and unlimited (grey line) and 5 and 95 percentiles for the dispersal-limited model (dashed lines). The species accumulation curves show the curves predicted by the dispersal-limited (solid line) and unlimited (grey line) and the 5 and 95 percentiles for observed SACs (derived by repeated sampling of J_L individuals). Parameter estimates are from one-stage single site analyses (Etienne 2005); although multiple likelihood maxima were found at the Crest and Laterite we show only the statistically most likely results here.

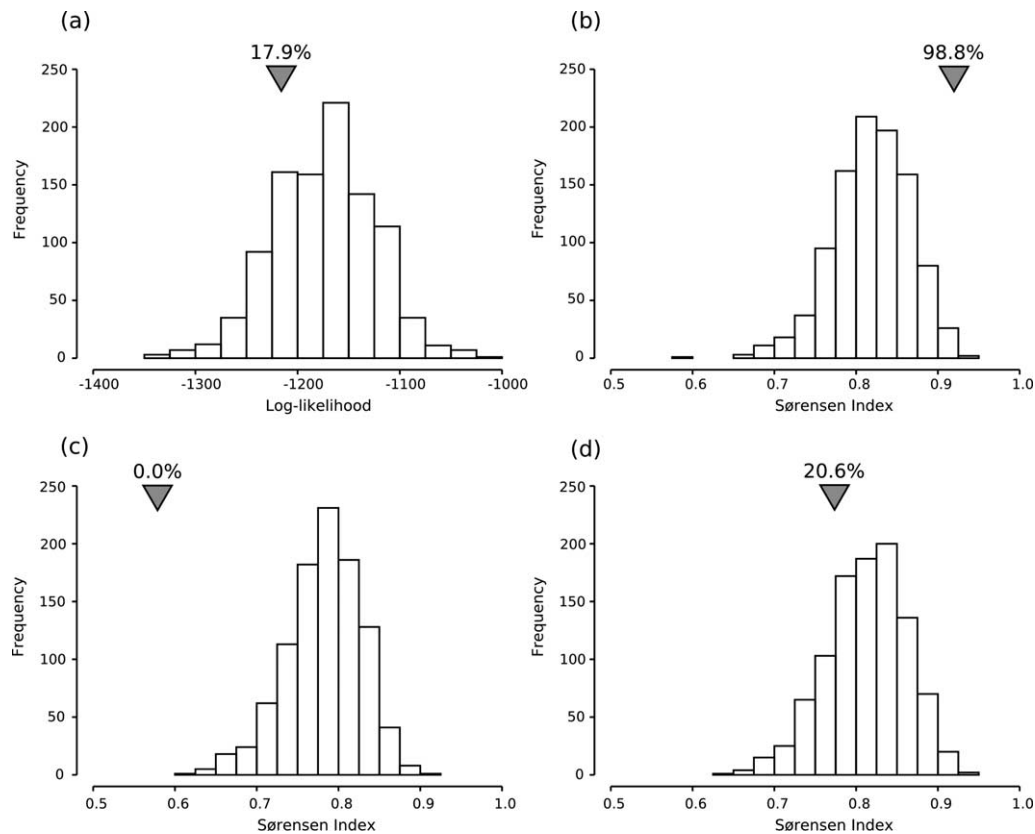


Figure 3. Tests of departure from neutrality based on Etienne’s (2007) ‘exact test’ using the parameters estimated from the observed data (Table 2). Departure from neutrality was assessed on the basis of comparison of (a) the observed log-likelihood with that of 1000 simulated neutral communities, and (b–d) the observed dissimilarity (Sørensen’s index) between site pairs (b – Crest–Laterite, c – Crest–Swale and d – Laterite–Swale), with the simulated neutral communities. Arrows show the position of the observed data in relation to the simulated neutral communities; values above the arrow show the percentage of simulated communities with values smaller than the observed.

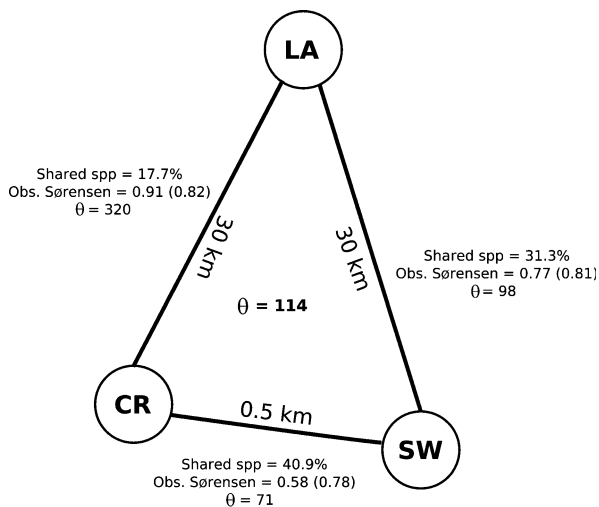


Figure 4. Schematic view of relationships between the three sites showing their arrangement in geographic space (not to scale), dissimilarities (Sørensen’s index) for observed and simulated neutral communities (number in parentheses), and θ from the three site (the metacommunity ‘mean’; bolded value in centre) and pairwise analyses (Cr = Crest; La = Laterite and Sw = Swale).

Based on the three-site estimates across all species, I-values are considerably higher at Crest than Laterite, and show little difference between Crest and Swale. In terms of the pairwise comparisons, I-values tend to follow the order Crest \approx Swale > Laterite. However, estimates of I for resprouters are similar at all sites, while for nonsprouters they are higher at Crest and lower at Laterite and Swale (Table 2). Below, we discuss in more detail the plausibility of these estimates in the light of independent knowledge of the system.

How plausible are neutral model estimates of metacommunity species richness, speciation and species longevity estimates under point mutation?

Our best estimate of vascular plant species richness on the Eneabba Plain is around 1100 species (based on available information from herbarium records); but this is likely an underestimate as floristic survey, species discovery and description are still very active fields in WA. Our estimate of θ yields a predicted metacommunity species richness $[E(S, \theta)]$ of 2054 species. If we estimate metacommunity richness solely from the core sandplain Crest and Swale site data, estimates of θ indicate an expected metacommunity richness of 1314. Based on the combined sample estimations

Table 4. Estimates of species richness, speciation (per generation) and expected longevity of a newly-arisen species under the point mutation model based on estimates of θ and J_M from the combined data. WF and H denote the Wright-Fisher and the Hubbell form of the neutral model, respectively $u = \text{speciation rate (probability) per generation}$ and $v = \text{the speciation rate (probability) per individual per time-step}$; $E[S] = \text{expected metacommunity species richness}$; 'species per generation' denotes the number of new species appearing in the metacommunity per generation under point mutation (abundance = 1). R and N denote resprouters and nonsprouters, respectively (estimates of J_M assume that 70% of individuals are resprouters).

	Parameters		Speciation (u)		Speciation (v)		E[S] WF/H	Species per generation WF/H	Longevity (generations) WF/H
	θ	J_M	WF	H	WF	H			
Combined	113.93	7.69×10^9	7.40×10^{-9}	1.92×10^{-18}	7.40×10^{-9}	1.48×10^{-8}	2,054	57	36
Combined: R	81.19	5.39×10^9	7.54×10^{-9}	2.80×10^{-18}	7.54×10^{-9}	1.51×10^{-8}	1,462	41	36
Combined: N	30.48	2.31×10^9	6.60×10^{-9}	5.72×10^{-18}	6.60×10^{-9}	1.32×10^{-8}	554	15	36

of θ for the resprouter and nonsprouter components of the community (Table 4), we find $E(S, \theta) = 1462$ and 554 for resprouters and nonsprouters, respectively. This yields a total metacommunity richness of 2016 and a resprouter fraction of 0.72 that is close to observed values (Enright et al. 2007). Under point mutation, the estimated species life-spans are rather low and the rate of species production per generation high (36 generations and 57, respectively; Table 4). For species with high abundances the time required to reach this abundance, by ecological drift alone and starting with an abundance of one, is extremely long (Table 5).

Do neutral model predictions of speciation rates in perennial nonsprouter and resprouter species agree with recent molecular phylogenies?

Based on the estimated θ value, speciation rates in the nonsprouters and resprouters are similar ($v_R/v_N = 1.14$; Table 4), as predicted by a recent molecular phylogeny (Verdú et al. 2007) and other analyses (Bond and Midgley 2003, Lamont and Wiens 2003).

Discussion

Comparison with other species-rich communities: species abundance distributions and neutral model parameters

The sclerophyll shrublands (kwongan) that we consider show species abundance distributions closer to those obtained for tropical rainforest communities than fynbos. Compared with the Latimer et al. (2005) fynbos sites, our kwongan sites show lower local dominance by a small number of species and a larger fraction of rare species. The two community-types are structurally similar and experience similar climatic conditions, although Hnatiuk and Hopkins (1981) point out that Cape Hangklip (a site considered by Latimer et al. 2005) receives nearly twice as much rainfall as Eneabba and encompasses a greater range of habitats due to higher altitudinal variation. Keeley and Fotheringham (2003) note that Californian chaparral communities (also Mediterranean-type) show less equitable community structure than Western Australian shrubland communities, attributing this to (1) the relative absence of annual species in the WA kwongan, and (2) the prevalence of resprouters in kwongan, lessening opportunities for turnover (in time). However, these arguments cannot satisfactorily explain differences between the Cape Floristic and the Southwest Floristic Regions as resprouters are common and annuals rare in both: indeed, the kwongan and the fynbos show remarkably convergent ecological characteristics (Cowling et al. 1996).

Our estimates of θ are comparable with those seen in some tropical rainforest and fynbos communities (Table 2). The combined sample analysis yielded an estimated θ of 114, compared with values of 60–150+ (tropical rain forest) and 30–350+ (Cape Floristic Region). We found θ values consistently higher than those reported for the single sample Barro Colorado Island (BCI) rainforest datasets but lower than for those datasets combined with other Central American rainforest communities (Etienne 2007). These

Table 5. Estimates of expected age of species (generations) with different abundances (x) under ecological drift; x = 0.144 is the abundance of the most abundant species at any of the three sites.

J_M	Relative abundance (x)				
	0.0001	0.001	0.01	0.1	0.144
7.69×10^9	1.417×10^7	1.064×10^8	7.158×10^8	3.937×10^9	5.017×10^9

differences occur despite similar numbers of individuals being sampled, albeit with finer-grained and geographically closer samples in our case. Our estimates of I and m are comparable with those from the Cape Floristic Region, and are two to three orders of magnitude smaller than those observed in some tropical rainforest communities (Latimer et al. 2005, Etienne et al. 2006). Note, however, that θ is influenced by the degree of similarity between local sites that is, at least in part, a function of the distance between sites, and edaphic differences. While these factors undoubtedly vary between the studies considered here, our estimates are ecologically plausible in a comparative sense.

Interpreting I: recruitment limitation or edaphic specialisation/fidelity?

There is considerable biological evidence for high speciation rates in the Southwest Floristic Region driven by edaphic separation between species (Hopper 1979, Hopper and Gioia 2004). Our analyses are in agreement with this evidence, as they suggest low rates of migration coupled with high rates of speciation in the Eneabba shrublands metacommunity. Many species on the Eneabba Plain have traits associated with highly localised dispersal and show fine-scale clumping (Perry et al. 2008), although even among these species there is evidence for long-distance dispersal (He et al. 2009a, 2009b). Since both edaphic specialisation and dispersal limitation appear to have a role in structuring the shrublands of the Eneabba Plain, the key question in interpreting these low estimates of migration rates is: how much of the inferred dispersal limitation results from edaphic fidelity as opposed to strict dispersal limitation?

Estimates of θ for the pairwise combinations reflect the edaphic and ecological relationships between sites when placed in the context of the three site metacommunity 'mean'. The Crest–Swale and Swale–Laterite pairs have θ values that are slightly lower than the 'mean', while the Crest–Laterite θ value is considerably higher. The Crest–Laterite sites are edaphically the most dissimilar. I values are considerably higher at Crest than Laterite, and are similar at Crest and Swale (Table 2). I measures recruitment limitation, which encompasses both dispersal limitation and establishment limitation (Jabot et al. 2008). The Laterite site is on the margin, and in a relatively lower rainfall area of the sandplain, so both processes could contribute to its lower I values. First, as sandplain species can only arrive from a limited number of directions and, second, if resident species are better adapted to the drought-prone shallow soils and lower rainfall of the site relative to at least some potential immigrant species, then the establishment likelihood will be lower in immigrants than in residents.

Strong dispersal limitation should result in the aggregation of species, and this is evident in these shrubland communities. For example, at Crest and Laterite 70% of species show significant conspecific aggregation at scales of 0 to 10 m, and this aggregation is strongest at short distances (Perry et al. 2008). While there are few physical barriers to dispersal on the Eneabba Plain, a number of species have dispersal syndromes typically associated with short dispersal distances, including those dispersed by ants (11% of the species assessed here have elaiosomes – Lamont et al. unpubl.), those limited to vegetative spread due to the loss of sexual reproduction (e.g. *Banksia elegans*), those with subterranean flowers (e.g. *Alexgeorgea subterranea*) or producing cones at ground-level that are prone to burial (e.g. *Banksia bipinnatifida* and *B. tridentata*). However, the extent of dispersal is confounded by edaphic preferences (Lamont et al. 1989). Hnatiuk and Hopkins (1981) concluded that the distribution of 74% of 338 species recorded in the same general area was edaphically controlled. While there may be reduced exchange between different substrate types, there may be more substantial movement between patches sharing the same substrate (Calviño-Cancela et al. 2008). This is similar to the 'bedrock' model described by Purves and Pacala (2005), although they focus on the extreme case of complete isolation of edaphic types, whereas on the Eneabba Plain edaphic fidelity varies between species. There is evidence that geographically separated sites that share similar edaphic conditions on the Eneabba sandplain experience significant genetic exchange via long-distance seed movement (He et al. 2004, Krauss et al. 2006). He et al. (2004, 2009a) estimate inter-population migration rates of 5–7% for two wind-dispersed *Banksia* species and a rate of 1.7% for the primarily ant-dispersed *Daviesia triflora* (He et al. 2009b) between dune crests up to 2.5 km apart. Our data (unpubl.) from 79 100 m² plots scattered across the Eneabba Plain show that 21% of woody plants recorded in 10 or more plots were either fully restricted to, or more than ten-times as likely to be present, either on dunes or in swales (χ^2 test, $p < 0.05$, Bonferroni-corrected). If this percentage also applies for the Crest and Swale sites examined here, and discounting the 41% species common to the two sites, then one-third of the species unique to either site may be due to substrate preference and two-thirds to dispersal limitation. Thus, the observed turnover in species may be explained by environmental variation and fidelity to edaphic substrate as well as by dispersal effects.

The exact test of neutrality that we used suggests that the form of the neutral model that we used (i.e. spatially implicit with point mutation speciation) can reproduce the observed species abundance distributions (Fig. 3a). Thus, we cannot reject this neutral model on these grounds. However, we re-iterate that failure to reject the model does

not mean that neutral processes are operating, rather that the model adequately reproduces observed patterns. The tests of neutrality do suggest that the turnover of species between sites (as measured by community dissimilarity) departs significantly from that expected under neutrality for two of the three site pairs (Fig. 3b–d). The Laterite–Swale pair shows dissimilarities consistent with those predicted by the neutral model, suggesting that edaphic differences between the two are minimal; this is the site pair with the most similar edaphic conditions. The Crest–Laterite pair is significantly more dissimilar than neutral processes (dispersal limitation) predict, suggesting that there are significant edaphic non-neutral differences between the two sites. The Crest–Swale pair is significantly more similar than the neutral model predicts. This suggests a strong common environmental filter (Jabot et al. 2008) at the two sites making them more equal than is expected under neutral processes alone. This is not the case, however, and the sites are edaphically quite different. It is more likely that the higher than expected similarity between the Crest and Swale sites is due to their proximity (500 m) allowing some level of direct dispersal between them. One of the assumptions of the neutral model is that distance between sites is large relative to the dispersal distance. It is possible that the Crest–Swale site pair violates this assumption.

We selected the Eneabba Plain as the site of our studies as it is species-rich and well differentiated from surrounding substrates, internally homogeneous and distant from similar substrates. This may be true relative to other areas of similar size nearby or even more distant within southwestern Australia, but it is especially more likely to be true relative to areas studied elsewhere, such as those of the vastly larger and more heterogeneous neotropical forests or Cape Floristic Region. Nevertheless, it does share species with nearby habitats and shows evidence of some internal habitat differentiation. Thus, while the conditions to qualify as a neutral metacommunity are as ideal as possible, local non-neutral processes clearly do play a role. These deviations from neutrality are partly picked up by the neutral model. Ultimately, however, these issues point to the inherent difficulties in using a spatially implicit neutral model in continuous and heterogeneous landscapes, and re-emphasise the need for the development of spatially explicit neutral models, despite the challenges that this poses (Etienne 2007, Leigh 2007, Rosindell et al. 2008).

Predictions of metacommunity species richness and speciation

The Eneabba Plain is clearly delimited in space. Thus, we can estimate metacommunity size (J_M) and species richness ($E[S, \theta]$) in a way that is not often possible and that, to our knowledge, has not been attempted previously. Some of the estimates produced by the neutral model are surprisingly accurate given the simplistic point mutation model from which they are derived. Our combined site estimate of θ predicts a metacommunity species richness of 2054. This is not unreasonably far from our independent (and no doubt under-) estimate of vascular plant metacommunity richness of approximately 1100 species (based on WA Herbarium records).

Relative rates of speciation in resprouters and nonsprouters (v_R/v_N) predicted from θ are also remarkably similar (the estimated speciation rate of nonsprouters is 0.88 times that of resprouters; Table 4). Because resprouters produce fewer seeds and are much longer lived than nonsprouters we might expect their speciation rate to be slower. However, recent frequency analyses by Lamont and Wiens (2003) and the molecular phylogeny of Verdú et al. (2007) suggest that relative rates of speciation in resprouters and nonsprouters are very similar, as predicted by our neutral-model based estimates of v (although, these estimates are sensitive to estimates of J_M for each group).

It has been argued that time is a critical problem for neutral models of community dynamics (Lande et al. 2003, Nee 2005, Ricklefs 2003, 2006). In particular, these authors note that under ecological drift (effectively a random walk in species abundances) the abundance of species will change slowly in large (i.e. high J_M) communities, such that the expected time to extinction is approximately J_M generations. While the extinction times of extant species are extremely long, this is less of a problem than the fact that the time to reach their current abundance under ecological drift – assuming that they start at a very low abundance as is the case under the point mutation model – is also extremely long. The most abundant species at any of our three sites is a *Schoenus* sp. (Cyperaceae) at Laterite, which has a relative abundance of 0.144, and using Eq. 6 (Etienne et al. 2007b) we estimate the ‘age’ of this species under pure ecological drift to be greater than 5×10^9 generations! Even a species with relative abundance of only 0.0001 is estimated to have an age in excess of 1.4×10^7 generations (Table 5). However, while the probability of a particular species reaching a large population size is low, there will have been, and are many species, so the probability that one species does so is higher. The expected times (Table 5) are averages and are influenced by all those species that take an extremely long time to reach that abundance. Thus, it would be more appropriate to consider a probability distribution of the expected times (or the median and other percentiles of that distribution), rather than just the expected average times. Currently, however, we are not aware of an expression for this distribution. Even though the expected time is highly implausible, this may not be the point: the point is whether some species can make it in a realistic time frame, and that is a question that the average values cannot fully address. Because these expected times may not be correct means that we cannot use them to refute (or accept) the neutral model.

Estimated rates of speciation are also problematic (Table 5). Based on estimated generation lengths (assuming that 70% of species are resprouters) and the prediction of approximately 30 new species arising each generation in a metacommunity comprising in the order of 1×10^{10} individuals and 1000 species, this equates to nine new nonsprouter species per generation (i.e. every 13 years)! The average lifetime of ‘new’ species is also short, averaging 36 generations (which equates to just 400–500 years for nonsprouters, assuming inter-fire interval approximates generation length, and 5000–11 000 years for resprouters, assuming longevities of 150–300 years). Ricklefs (2003) points out that one problem with the point mutation model is that it suggests that the bulk of species will be very rare

(population size close to one) and likely cryptic. This explains why average species longevity is so short and why it seems that there are so many species arising under the point mutation model – most species are never observed as they are extremely rare and rapidly go extinct (Hubbell 2003).

Recently, Zillio and Condit (2007) suggested that temporal scaling of neutral models is perhaps not as problematic as has been argued. Using a spatial generalisation of Hubbell's neutral model, they found that even when starting from the worst-case position (i.e. complete dominance of a local community by a single species) community descriptors such as species richness and the shape of the species abundance distribution can reach an equilibrium in 10 000 generations (in our case 130 000–300 000 years). This is because time to reach equilibrium species richness and abundance, unlike time to extinction, is independent of the size of the community. Furthermore, although the Wright–Fisher, Moran and Hubbell forms of the neutral model have different time-scales, and so do zero-sum and non-zero-sum forms (Etienne and Alonso 2007, Haegeman and Etienne 2008), their equilibrium abundance distribution is identical. Thus, even if the temporal dynamics are not correct in the current form of the neutral model, the equilibrium predictions that we use are extremely robust. In fact, Blythe and McKane (2007) argue that this is so for any neutral model under mild conditions, a property called the robustness of the coalescent (Möhle 2000). It is possible that a neutral model incorporating environmental stochasticity may have a more realistic time-scale, although how such a model could be found is unclear.

We might reconcile the predictions of the neutral model with the dynamics of the Eneabba Plain metacommunity by considering (1) what is meant by 'speciation', v , and (2) the nature of ecological drift in this system. Speciation can be viewed as the 'introduction' of species into the metacommunity. This encompasses the birth of new species and the dispersal of existing species into the metacommunity (Chave and Leigh Jr. 2002, Zillio and Condit 2007). Such long-distance dispersal is a potential mechanism buffering species present in low abundances against extinction: it is a rescue effect. Second, drift in systems structured by landscape-level disturbances is somewhat different to the dynamics of tropical rainforests in which Hubbell's neutral theory has been most extensively tested. In our system the entire local community periodically experiences disturbance by fire with a significant component of the system (including all nonsprouters) dying in each event. The extent to which a species' abundance after a fire event is correlated with its abundance pre-fire is uncertain, although Enright et al. (2007) report a significant positive correlation between seed store sizes at the time of fire, and pre-fire abundances for plant species in the study sites described here.

Conclusions

The neutral model proposed by Hubbell (2001) can potentially provide useful estimates on the rates of speciation and species migration in a community. Using analytical methods for the exact solution of Hubbell's spatially implicit

neutral model with point mutation speciation we show that the species-rich shrubland (kwongan) communities of the South West Floristic Region of Western Australia have high speciation rates. However, rates of speciation are not as high as those described for some ecologically similar fynbos communities in the Cape Province Floristic Region of South Africa (Latimer et al. 2005, Etienne et al. 2006). While the model's parameters suggest low dispersal rates, the biological evidence for this is more equivocal, and is confounded by subtle but significant substrate variation across the landscape. The estimates produced by the neutral model, when converted into temporally-scaled speciation and species longevity rates, are implausible. However, under point mutation the neutral model produces surprisingly good estimates of metacommunity species richness, and the relative rates of speciation in nonsprouting and resprouting species agree with a recent frequency analysis and a molecular phylogeny for these groups. The parameter values also contain useful information about the relative contribution of dispersal, establishment and edaphic conditions in structuring the communities of the Eneabba Plain. We conclude that neutral models parameterised on the basis of snapshot abundance data do, when evaluated carefully, have the potential to be informative about the dynamics of natural systems.

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References

- Alonso, D. et al. 2006. On the merits of neutral theory. – *Trends Ecol. Evol.* 21: 451–458.
- Blythe, R. A. and McKane, A. J. 2007. Stochastic models of evolution in genetics, ecology and linguistics. – *J. Stat. Mech. Theory Exp.* P07018.
- Bond, W. J. and Midgley, J. J. 2003. The evolutionary ecology of sprouting in woody plants. – *Int. J. Plant Sci.* 164: S103–S114.
- Calviño-Cancela, M. et al. 2008. Distribution of myrmecochorous species over the landscape and their potential long-distance dispersal by emus and kangaroos. – *Div. Distr.* 14: 11–17.
- Caswell, H. 1976. Community structure: a neutral model analysis. – *Ecol. Monogr.* 46: 327–354.
- Chave, J. 2004. Neutral theory and community ecology. – *Ecol. Lett.* 7: 241–253.
- Chave, J. and Leigh Jr., E. G. 2002. A spatially explicit neutral model of β -diversity in tropical forests. – *Theor. Popul. Biol.* 62: 153–168.
- Chiarucci, A. et al. 2003. Performance of nonparametric species richness estimators in a high diversity plant community. – *Div. Distr.* 9: 283–295.

- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. – *Ecol. Lett.* 8: 1175–1182.
- Cowling, R. W. and Lamont, B. B. 1998. On the nature of Gondwanan species flocks: diversity of Proteaceae in Mediterranean southwestern Australia and South Africa. – *Aust. J. Bot.* 46: 335–355.
- Cowling, R. W. et al. 1996. Plant diversity in Mediterranean-climate regions. – *Trends Ecol. Evol.* 11: 362–366.
- Enright, N. J. et al. 2007. 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. – *Ecol. Lett.* 8: 253–260.
- Etienne, R. S. 2007. A neutral sampling formula for multiple samples and an ‘exact’ test of neutrality. – *Ecol. Lett.* 10: 608–618.
- Etienne, R. S. 2009a. Improved estimation of neutral model parameters for multiple samples with different degrees of dispersal limitation. – *Ecology* 90: 847–852.
- Etienne, R. S. 2009b. Maximum likelihood estimation of neutral model parameters for multiple samples with different degrees of dispersal limitation. – *J. Theor. Biol.* 257: 510–514.
- Etienne, R. S. and Olff, H. 2004. How dispersal limitation shapes species–body size distributions in local communities. – *Am. Nat.* 163: 69–83.
- Etienne, R. S. and Alonso, D. 2005. A dispersal-limited sampling theory for species and alleles. – *Ecol. Lett.* 8: 1147–1156.
- Etienne, R. S. and Alonso, D. 2007. Neutral community theory: how stochasticity and dispersal-limitation can explain species coexistence. – *J. Stat. Phys.* 124: 485–510.
- Etienne, R. S. et al. 2006. Comment on “Neutral theory reveals isolation and rapid speciation in a biodiversity hotspot”. – *Science* 311: 610b.
- Etienne, R. S. et al. 2007a. The zero-sum assumption in neutral biodiversity theory. – *J. Theor. Biol.* 248: 522–536.
- Etienne, R. S. et al. 2007b. Modes of speciation and the neutral theory of biodiversity. – *Oikos* 116: 241–258.
- Haegeman, B. and Etienne, R. S. 2008. Relaxing the zero-sum assumption in neutral biodiversity theory. – *J. Theor. Biol.* 252: 288–294.
- He, T. et al. 2004. Long distance seed dispersal in a metapopulation of *Banksia hookeriana* inferred from a population allocation analysis of AFLP data. – *Mol. Ecol.* 13: 1099–1109.
- He, T. et al. 2009a. Long-distance dispersal among seed populations of *Banksia attenuata* a fire-surviving species in southwestern Australia. – *Ecography*, in press.
- He, T. et al. 2009b. Ants cannot account for inter-population dispersal of the arillate pea *Daviesia triflora*. – *New Phytol.* 181: 725–733.
- Hnatiuk, R. J. and Hopkins, A. J. M. 1981. An ecological analysis of kwongan vegetation south of Eneabba, Western Australia. – *Aust. J. Ecol.* 6: 423–438.
- Holyoak, M. and Loreau, M. 2006. Reconciling empirical ecology with neutral community models. – *Ecology* 87: 1370–1377.
- Hopper, S. D. 1979. Biogeographical aspects of speciation in the southwest Australian flora. – *Annu. Rev. Ecol. Syst.* 10: 399–422.
- Hopper, S. D. and Gioia, P. 2004. The southwestern Australian floristic region: evolution and conservation of a global hot spot of biodiversity. – *Annu. Rev. Ecol. Syst.* 35: 623–650.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.
- Hubbell, S. P. 2003. Modes of speciation and the lifespans of species under neutrality: a response to the comment of Robert E. Ricklefs. – *Oikos* 100: 193–199.
- Hubbell, S. P. 2006. Neutral theory and the evolution of ecological equivalence. – *Ecology* 87: 1387–1398.
- Jabot, F. et al. 2008. Reconciling neutral community models and environmental filtering: theory and an empirical test. – *Oikos* 117: 1308–1320.
- Keeley, J. E. and Fotheringham, C. J. 2003. Species–area relationships in Mediterranean-climate plant communities. – *J. Biogeogr.* 30: 1629–1657.
- Krauss, S. L. et al. 2006. Late Quaternary climate change and spatial genetic structure in the shrub *Banksia hookeriana*. – *Mol. Ecol.* 15: 1125–1137.
- Lamont, B. B. and Wiens, D. 2003. Are seed set and speciation rates always low among species that resprout after fire, and why? – *Evol. Ecol.* 17: 277–292.
- Lamont, B. B. et al. 1989. Coexistence and competitive exclusion of *Banksia hookeriana* in the presence of congeneric seedlings along a topographic gradient. – *Oikos* 56: 39–42.
- Lande, R. et al. 2003. Stochastic population dynamics in ecology and conservation. – Oxford Univ. Press.
- Latimer, A. M. et al. 2005. Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hotspot. – *Science* 309: 1722–1725.
- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Leigh, E. G. 2007. Neutral theory: a historical perspective. – *J. Evol. Biol.* 20: 2075–2091.
- Maurer, B. A. and McGill, B. J. 2004. Neutral and non-neutral macroecology. – *Basic Appl. Ecol.* 5: 413–422.
- McGill, B. 2003. Strong and weak tests of macroecological theory. – *Oikos* 102: 679–685.
- McGill, B. J. et al. 2006. Empirical evaluation of neutral theory. – *Ecology* 87: 1141–1423.
- Miller, B. P. et al. 2007. Record error and range contraction, real and imagined, in the restricted shrub *Banksia hookeriana* in south-western Australia. – *Div. Distr.* 13: 406–417.
- Möhle, M. 2000. Ancestral processes in population genetics – the coalescent. – *J. Theor. Biol.* 204: 629–638.
- Munoz, F. et al. 2007. Estimating parameters of neutral communities from one single large to several small samples. – *Ecology* 88: 2482–2488.
- Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. – *Nature* 403: 853–858.
- Nee, S. 2005. The neutral theory of biodiversity: do the numbers add up? – *Funct. Ecol.* 19: 173–176.
- Oreskes, N. et al. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. – *Science* 263: 641–646.
- Perry, G. L. W. et al. 2008. Spatial patterns in species-rich sclerophyll shrublands of southwestern Australia. – *J. Veg. Sci.* 19: 705–716.
- Purves, D. W. and Pacala, S. W. 2005. Ecological drift in niche-structured communities: neutral pattern does not imply neutral process. – In: Burslem, D. et al. (eds), *Biotic interactions in the tropics*. Cambridge Univ. Press, pp. 107–138.
- Ricklefs, R. E. 2003. A comment on Hubbell’s zero-sum ecological drift model. – *Oikos* 100: 185–192.
- Ricklefs, R. E. 2006. The unified neutral theory of biodiversity: do the numbers add up? – *Ecology* 87: 1424–1431.
- Rosindell, J. et al. 2008. A coalescence approach to spatial neutral ecology. – *Ecol. Inf.* 3: 259–271.
- Vallade, M. and Houchmandzadeh, B. 2003. Analytical solution of a neutral model of biodiversity. – *Phys. Rev. E* 68: 061902–061905.

- Verdú, M. et al. 2007. Burning phylogenies: fire molecular evolutionary rates and diversification. – *Evolution* 61: 2195–2204.
- Volkov, I. et al. 2005. Density dependence explains tree species abundance and diversity in tropical forests. – *Nature* 438: 658–661.
- Walker, S. C. 2007. When and why do non-neutral metacommunities appear neutral? – *Theor. Popul. Biol.* 71: 318–331.
- Walker, S. C. and Cyr, H. 2007. Testing the standard neutral model of biodiversity in lake communities. – *Oikos* 116: 143–155.
- Zillio, T. and Condit, R. 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. – *Oikos* 116: 931–940.