The frequency of metapopulations, metacommunities and nestedness in a fragmented landscape

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Metapopulation and metacommunity theory may be extremely useful for understanding community composition and species distributions in fragmented landscapes. However, how well particular spatial ecological models represent natural systems is not known and so the general importance of those models is unclear. In three naturally fragmented landscapes in Tasmania, Australia, I sampled beetles from 67 sites, including continuous forest, small forest patches in a sedgeland matrix, streamside forest, and the matrix. Of forty commonly captured beetle species, at least 37% do not form metapopulations of any kind because they do not disperse far enough, disperse too far, or occur in the matrix. Only 7.5% of the species showed distributions consistent with a mainland-island metapopulation, which was surprising given the mainland-island structure of the landscape. These patterns were also consistent with a classic metapopulation. Deterministic metapopulations were probably common, involving at least 32% of species. Most predicted metacommunity patterns were not observed because only subsets of the fauna followed a particular metacommunity model. Seven, mostly flying, species were influenced only by habitat quality, supporting the Species-sorting or Mass-effects models, and the strong distinction between the beetle fauna of *Eucalyptus* patches and the matrix suggested an over-riding influence of a Species-sorting process. Seven, mostly flightless, species showed a negative relationship with increasing patch isolation, while another six, mostly flying, species showed the opposite pattern, with higher frequency of occurrence in more isolated patches. Both groups were strongly nested. The flying species were probably excluded from less isolated sites through interactions with poor dispersers, providing a novel mechanism leading to a nested distribution. The Patch-dynamics and Species-sorting processes were equally consistent with the pattern, emphasizing that these models are relatively simplistic when confronted with real community data. Additional complexity needs to be built into the models to accommodate the diverse patterns observed in natural communities.

Dispersal ability can influence whether or not a species declines in fragmented landscapes (de Vries et al. 1996, Driscoll and Weir 2005). The important role of dispersal is recognized in a range of ecological theory currently employed in conservation biology. Dispersal strongly influences the risk of species extinction in metapopulation theory (Hanski 1998) and dispersal drives processes that influence a range of community patterns under metacommunity theory (Leibold et al. 2004), including the formation of nested subsets (Patterson 1990). However, the prevalence of particular mechanisms described by these theories is poorly understood because few studies have attempted to examine metapopulation or metacommunity frequency among a suite of species in the same patchy landscape (but see Nieminen and Hanski 1998, Cottenie et al. 2003, Verheyen et al. 2004, Dahlgren and Ehrlén 2005, Vanschoenwinkel et al. 2007). With knowledge of the expected patterns under each theory, it is possible to use field data to discriminate among competing models and so to build a clearer understanding of the importance of competing theories.

Metapopulation theory has been widely used to assess extinction risks in modified landscapes (Hanski 1998, Hanski and Gaggiotti 2004). Although a continuum of metapopulation dynamics is possible (Hanski and Gaggiotti 2004), Harrison (1991) identified four categories of spatial dynamics and these remain a valuable research framework (Driscoll in press). Harrison's (1991) categories were: (1) Classic metapopulations (Levins 1970) where populations in discrete habitat patches undergo extinction and recolonization dynamics; (2) Mainland-island and Source-sink metapopulations where a permanently occupied patch is surrounded by temporary populations; (3) Patchy populations where there is very high migration between habitat patches forming a single population; (4) Non-equilibrium populations where species undergo widespread range expansion or decline. In addition, 'deterministic metapopulations' occur when species' occurrence is determined by habitat patch condition (Thomas 1994). Although there are examples of natural metapopulations, there is substantial debate about the prevalence of metapopulations in nature (Harrison and Taylor 1997, Baguette 2004, Hanski and

Gaggiotti 2004, Driscoll 2005, Driscoll in press). For example, Fahrig (2003) could find little evidence supporting a fragmentation effect, implying that dispersal, and therefore metapopulation dynamics, may not be a key process influencing the survival of species in fragmented habitats.

An extension of metapopulation concepts to the community level led to metacommunity theory, where a set of local communities is connected by dispersal (Gilpin and Hanski 1991). There are four commonly discussed metacommunity models (Leibold et al. 2004). Under the Patch-dynamics model, community composition in habitat patches is determined by a tradeoff between dispersal ability and competitive or predatory power. The model assumes that species dominance is inversely related to dispersal ability (Tilman et al. 1994), and that habitat quality is constant across patches (Leibold et al. 2004). In contrast, the Species-sorting metacommunity model assumes that patch quality varies and species are closely adapted to particular environmental conditions (Chave et al. 2002, Urban 2004). The Mass-effects model is where immigration primarily determines local abundance (source-sink systems) (Cottenie 2005). The fourth category is the Neutral model, where species have equal competitive abilities, and persistence in a community can be described by a random sampling function (Bell 2001, Hubbell 2001). The result is that species composition in a community drifts in a way that is analogous to genetic drift in neutral genetics models (Chave 2004, Bell et al. 2006). The four metacommunity categories are not always distinct, and merge under certain conditions. For example, with very high dispersal, the Mass-effects model is effectively equivalent to a Neutral model (Cottenie 2005), but with low dispersal, the Mass-effects model approaches a Species-sorting process. Studies from highly connected pools suggest that Species-sorting and Mass-effects are common among pool-dwelling invertebrates (Cottenie et al. 2003, Vanschoenwinkel et al. 2007). However, more generally the importance of competing metacommunity theories is yet to be established (Holyoak et al. 2005).

Nested patterns can emerge from certain metacommunity processes (Worthen 1996, Wright et al. 1998, Bloch et al. 2007) and so can be used to help distinguish among competing metacommunity models. In nested metacommunities, species that occur on species-poor sites are a predictable subset of the species from more diverse sites (Patterson and Atmar 1986). Four processes are commonly identified as producing nested patterns (Wright et al. 1998) including passive sampling by area (MacNally and Brown 2001), nested habitat quality (Honnay et al. 1999); extinction based on patch area or condition (Bolger et al. 1991, Lomolino 1996); or differential colonization ability (Kadmon 1995). Often only a proportion of the biota shows strong nesting patterns (Fischer and Lindenmayer 2005). The frequency and cause of nested patterns in natural communities remains uncertain (Boecklen 1997, Fischer and Lindenmayer 2005).

In this study, I investigate the importance of metapopulations, metacommunities, and nestedness by examining the distribution of beetle species in natural habitat patches with different levels of isolation and in three replicate landscapes. I use the three general areas of ecological theory

(metapopulations, metacommunities, nested-subsets) to enhance their integration and to avoid reinvention of theory using different terminology.

I will show that a large proportion of species do not form metapopulations in the study landscape but that many species may have deterministic metapopulations. Patch-dynamics and Species-sorting processes are most evident in the data set, including the pattern of nestedness predicted under the Patch-dynamics model.

Distinguishing among models

For investigating metapopulation theory, I allocate 40 common beetle species to a metapopulation model, based on their presence or abundance in the matrix, and the influence of patch isolation and habitat type. I assumed that non-equilibrium metapopulations (Harrison 1991) are unlikely to be found in the naturally fragmented study landscape because it has not been recently fragmented. I measure the extent of nestedness in the community, which I also use to help distinguish among metacommunity concepts.

For a landscape with increasing patch isolation, metacommunity theory makes the following predictions based on published analyses and some speculation about nested patterns.

Neutral

Fewer species, higher divergence between local communities and no relationships with habitat parameters (Hubbell 2001). Species most vulnerable to decline after fragmentation are rare before fragmentation (Hubbell 2001). A nested subset pattern is likely to develop when rare species consistently become extinct from isolated sites.

Patch-dynamics

Better dispersers that are poorer competitors or prey species will have higher incidence in more isolated sites, while an alternate set of species (poorer dispersers, superior species) will have higher incidence in less isolated sites (Tilman et al. 1994, Moilanen and Hanski 1995, Huxel and Hastings 1998). Relegation of good dispersers to isolated sites and confinement of poor dispersers to least isolated sites will lead to separate nested-subsets for those two groups of species.

Mass-effects

Individual species should show an interaction between isolation and habitat condition, with weak relationships at low distances due to mass movement of animals between habitats, but stronger relationships in more isolated sites as the system approaches a Species-sorting model (Mouquet and Loreau 2003, Chase et al. 2005). Species diversity should be lower in more isolated sites due to competitive exclusion by the locally best competitor and lack of immigration (Mouquet and Loreau 2003). Nested subset patterns are generally not expected because mass movement enables frequent mixing of populations. However nestedness is possible among the most isolated sites if habitat type is nested.

Species-sorting

There should be no relationship with isolation, but a strong relationship with habitat (Chase et al. 2005). No nested relationship is expected except if habitat type is nested, in which case fauna nestedness should not reflect patterns of patch isolation, but should correspond with an environmental gradient.

Methods

Study system

Sedgeland dominated by buttongrass *Gymnoschoenus sphaerocephalus* and heaths (Epacridaceae) cover 17% of the state of Tasmania (Jackson 1999). Forest species that can survive within buttongrass sedgelands are those with extensive lignotubers allowing vegetative regeneration after fire (Jackson 1999). *Eucalyptus nitida* regenerates from lignotubers and forms small patches, often less than a hectare, throughout the buttongrass (Jackson 1999). The *Eucalyptus* scrub patches have an overstorey of multi-stemmed *E. nitida* usually <10 m tall, a dense midstorey up to 3 m high of *Banksia marginata* and *Leptospermum* species, with the entangling shrub *Bauera rubioides*, and sword grass *Gahnia grandis* frequently combining to create difficult field conditions. Annual rainfall is approximately 2500 mm.

Eucalyptus nitida patches occur at the margins of continuous forest, as strips along streams and as small patches completely surrounded by buttongrass. Although the age of patches is not known, they are likely to be old on a timescale of beetle generations. The patches have not been altered by recent human activity and because the patches regenerate from lignotubers after fire, they will have survived past conflagrations. Examination of aerial photographs showed consistent patch arrangement and size spanning a 40 year period.

Sampling

At each of three locations (North, Anne, Scotts), habitat patches from seven landscape elements were sampled, including (1) Connected: *Eucalyptus* scrub at the edge of continuous forest; (2) Close: small patches of scrub within 100 m of continuous forest; (3) Mid: small patches of scrub 100–420 m from continuous forest; (4) Distant: small patches of scrub 420–780 m from continuous forest; (5) Dense: small patches of scrub with several other small patches within 50 m; (6) Stream: linear scrub along streams surrounded by buttongrass; (7) Matrix: buttongrass sampled 20–100 m from nearest scrub patch (Fig. 1). Each landscape element was replicated three times at each location, with the exceptions of North (three Distant, four Mid), Anne (five Distant, two Mid), Scotts (six Distant,

Fig. 1. The study was conducted in *Eucalyptus* scrub patches and continuous forest (dark grey) surrounded by buttongrass sedgeland (light areas) in three locations. Sample sites were classified into one of seven landscape elements: 1 Connected; 2 Close; 3 Mid; 4 Distant; 5 Dense; 6 Stream; 7 Buttongrass matrix. Diagonally hashed areas at Scotts indicate cleared land associated with hydro-electric dams (vertically hashed). Grey and black dotted line indicates Scotts Peak Road.

two Mid). The cut-off distance between Mid and Distant sites was selected to ensure at least two sites in each category at each location. A total of 58 bush sites and nine buttongrass sites were sampled. All discrete patches (Close, Mid, and Distant landscape elements) were small (mean size 689 m², range 245–1211 m²). Elevation ranged from 300 to 400 m above sea level.

Each site was sampled using 16 pairs of 225 ml pit-fall traps (32 cups per site), spaced at 5 m intervals and with 50 ml of saturated salt solution as a preservative. Plastic lids held 5 cm above the ground prevented traps from filling with rain. Traps were set in December 2002 and left open for eight consecutive weeks over summer, when beetle activity is highest (Driscoll unpubl.). Although pit-fall trap capture rates can depend on the surrounding vegetation (Lang 2000), all of the bush sites had open habitat at ground level, so biases are likely to be minimal (also discussed in Driscoll 2005).

The collections were sorted to morphospecies then identified as far as possible. Most Staphylinidae were excluded from the data set because they are difficult to distinguish morphologically, although one common, distinctive taxon *Baeocera* sp. A was included.

All plant species were identified within the area spanned by pitfall traps and their percentage cover estimated in three categories (<20%, 20–50%, >50%).

Analysis

Plant and beetle community overview using MDS

Scrub sites were included in a non-metric multidimensional scaling (MDS) using a Bray-Curtis distance matrix derived from the plant species data. I used multiple starts of the MDS procedure to avoid local minima. New starts were continued until the stress had not been reduced for 100 successive iterations. The maximum iterations was 200, and convergence tolerance 10⁻⁷. Procrustes rotation was performed so that most of the variation was captured in axis 1. The three axes obtained were used as habitat factors in the Generalized linear model described below. Data were analysed using R ver. 2.0.1 including packages MASS (Venables and Ripley 2002) and vegan (Oksanen et al. 2007).

MDS was also used to obtain an overview of beetle community divergence. The magnitude of divergence between landscape elements for both the plant and beetle distance matrices were estimated using Clarke's (1993) R statistic, and the significance of differences between pairs of landscape elements was estimated using 5000 permutations of the data (Clarke 1993) (also called ANOSIM). R values usually range from 0 (no difference) to 1 (all between distances bigger than all within distances) (Chapman and Underwood 1999).

Beetle species distributions using GLM

Possible metapopulation types were inferred by examining the distribution of beetles among the landscape elements and the matrix. Beetle species analyzed were present at all

three locations and occurred on a total of nine or more sites. This arbitrary cut off enabled detection of species that specialize in one habitat, such as streams (three replicates at each of three locations). For these species, presence/absence data were analyzed using binomial Generalized linear models (GLM) with a logit link function (McCullagh and Nelder 1989). Location was fitted to each model first to remove that source of variation, then nine parameters were fitted in a forwards stepwise manner using the Step procedure of R 2.0.1. Five of the parameters enabled discrimination among the different landscape elements and were (levels in parentheses): Connected (connected to large forest tracts = connected, not connected to large forest tracts = other), Close (within 100 m of large forest tracts = close, all other sites = other), Isolation (420–780 m from large forest tracts = distant, 100–420 m from large forest tracts = mid, all other sites = other), Dense (among a dense area of scrub = dense, not among dense scrub = not), Stream (linear scrub along a stream = stream, not linear streamside = other). The three axes of a 3-D MDS representing vegetation at each site were also included (described above). The ninth parameter was patch area. Connected, Dense and Stream sites did not have a meaningful patch area and so were assigned the mean area of the discrete patches (Close, Mid and Distant sites; mean area 689 m²). This meant that factor Area was available to identify any area effects among the Close, Mid and Distant patches.

Species that were very widespread (absent from <9 sites, *Thalycrodes* sp. 1, *T. cylindricus*, *Palimboldus victoriana*), were analyzed using abundance in a Poisson GLM with log-link function, following the protocols used for the binomial models (McCullagh and Nelder 1989).

Results are reported where the deviance explained by the fitted factor was at least 10% of total deviance and $p < 0.05$. This criterion was applied so that only relationships explaining a substantial amount of variation are considered, and to minimize the risk of interpreting 'noise' factors that are often selected in stepwise procedures (Derksen and Keselman 1992).

Factors explaining at least 10% of variation were tested for an interaction with Location to see if the main effect was consistent in the three replicate landscapes. Some landscape elements were located near to each other within Location and so space may be confounded with landscape element. Testing for an interaction between Location and landscape elements will identify cases where spatial autocorrelation exists within Location.

To check for correlations between the plant MDS axes and the landscape elements (Connected, Close, Isolation, Dense, Stream, Location), I used each MDS axis as the dependent variable in stepwise models, described above. The only differences were that Location was fitted as an alternative and an ANOVA model was applied (normal error distribution, identity link function). Where 10% or more of the variation in MDS axes was explained by one of the landscape elements, there is the potential for confounding landscape element and vegetation in the stepwise models. To identify the independent variation explained by an MDS axis and by its correlated landscape element, I used Hierarchical partitioning (Chevan and Sutherland

1991). This was completed using `hier.part` in R statistical software (MacNally and Walsh 2004).

Metapopulation responses

The 40 common beetle taxa were allocated to one of eight (a–h) possible outcomes based on the above GLMs. Three outcomes were not metapopulations: species that did not occur significantly less frequently in the matrix (Fisher's exact test) (outcome a); ubiquitous species with frequency of occurrence > 0.9 in the patches (outcome b); species that were absent from all isolated sites implying dispersal is too low for metapopulation dynamics among patches (outcome c). Species that did not meet any of those criteria formed some kind of metapopulation or could not be classified. Patterns consistent with classic or mainland-island metapopulations were those where species occurred in isolated sites at reduced frequency (outcome d). Species with highest frequency in isolated sites (outcome e) or with significantly different frequency in mid sites (outcome f) were classed as deterministic metapopulations based on presumed interactions with other taxa. Species with no relationship with patch isolation but with significant relationship with vegetation parameters were classed as deterministic metapopulations based on habitat quality (outcome g). Species classed as indeterminate had no relationships with patch isolation or vegetation (outcome h).

Dispersal, Presence in the Matrix and Response category

A binomial GLM with logit link-function was used to examine the relationship between flight ability of beetles or presence in the matrix with response to landscape elements, as determined in the GLM (described above). I fitted presence/absence of functional wings, presence/absence in buttongrass matrix, and the interaction of those factors to explain the distribution of species among five response categories; decline with distance, increase with distance, low or high occurrence in sites of intermediate isolation (interaction), influenced by vegetation or no response. Species allocated to two response categories (vegetation and spatial) were classed using the response that explained the most variation in the GLM.

Nested subset analysis

I used the approach taken by Fischer and Lindenmayer (2005) to test for nestedness, which is simple to calculate (Brualdi and Sanderson 1999), allows comparison of different sized matrices (Wright and Reeves 1992), and uses an appropriate null model (Jonsson 2001). As an index of nestedness, I calculated Brualdi and Sanderson's (1999) discrepancy. With rows (sites) and columns (species) sorted from highest to lowest values, discrepancy is the number of presences that would need to be shifted to the left to generate a perfectly nested data set. I created the random data for each species in the matrix by sampling randomly, with probability equal to the fraction of sites occupied. Using this method, a given species had the same probability

of occurrence on any site (species randomly allocated across sites), but different species had separate probabilities of occurrence (Jonsson 2001, Fischer and Lindenmayer 2005). Five thousand random data sets were generated to estimate the probability of obtaining the observed discrepancy by chance. The mean discrepancy of the random data was used as the expected values in Wright and Reeves' (1992) formula for standardizing nested indices: percent nestedness = (expected discrepancy - actual discrepancy) / expected discrepancy (Fischer and Lindenmayer 2005). This method of scaling for matrix size is approximately linear for matrices with more than 200 cells (Fischer and Lindenmayer 2005), and all matrices that I examined were larger than that. Percent nestedness can be negative where sites are overdispersed compared with random data.

Additional metacommunity analyses

To examine the Neutral model's prediction of higher divergence among communities in more isolated sites, I calculated the average Bray-Curtis distance (plus SD) for pair-wise comparisons of sites within landscape elements.

The neutral model also predicted that regionally rare species should decline from more isolated sites, and this could lead to a nested subset pattern. I designated regionally rare species as those occurring on $\leq 1/3$ of Close, Dense or Connected sites. I then compared the proportion of rare species that declined with isolation (found using the GLM above) with the proportion of non-rare species that declined. It is possible that "rare" species are not rare because capture in pit-traps is dependent on movement in addition to population density. Non-significant results in this test may therefore arise because neutral processes are not acting or because rare species were misidentified.

Neutral and Mass-effects models predicted lower species richness in isolated patches, so I used species richness as the dependent variable in the stepwise Poisson GLM described above.

The Mass-effects model predicted an interaction between isolation and patch condition. I used a binomial or Poisson GLM to test for the interaction between MDS vegetation axes and isolation, after fitting the two main effects. A new factor, Isolation 2, was used and included Connected, Close and Dense sites in one level (not isolated) and Mid and Distant sites in the second level (isolated sites). Presence or abundance of each of 40 common beetle species was used as the dependent variable. Over-dispersion in the models was accommodated by estimating F as the mean deviance divided by the residual mean deviance and results were considered significant when $p < 0.05$ (McCullagh and Nelder 1989).

If Mass-effects grade into Species-sorting at high isolation and habitat is nested, a nested relationship may arise among the isolated sites. To explore this, I applied the nested analysis described above to a subset of sites including only mid and distant sites.

Results

From a collection of 10 343 individuals I identified 224 beetle morphospecies, 40 of which occurred at all three

locations and at nine or more sites (Appendix 1). Of 110 morphospecies occurring on three or more sites, two were only captured in the buttongrass matrix, 21 were captured in the matrix and the *Eucalyptus* scrub patches, and 87 were captured only in the patches. In two-dimensional ordination space, the beetle fauna from buttongrass sites did not overlap with the faunas from *Eucalyptus* patches and formed a separate cluster (results not shown, ANOSIM $R=0.82$, $p<0.0002$). This confirms results from different sites in the preceding year (Driscoll 2005).

Plant and beetle community overview

The only discernible divergence among plant communities was that streams tended to be outliers in ordination space (results not shown). ANOSIM analysis confirmed that streams had significantly divergent vegetation (Table 1). Lower but significant R values were obtained when comparing Connected-Mid, Connected-Distant and Dense-Distant.

Beetle communities were also significantly divergent in Streams (Table 1). However, in contrast with the plant data, almost all pair-wise comparisons indicated significant divergence among landscape elements (Table 1).

For the plant data, MDS axis 1 was significantly correlated with Stream (% deviance explained = 20%), axis 2 with Stream (25%) and axis 3 with Location (37%) and Stream (8%). Streams had lower values on all MDS axis than other landscape elements. Location differences are not the focus of this paper, and are not investigated further. However for stepwise analyses of beetle data (see below), when Stream, MDS axis 1, 2 or 3 explained >10% of the deviance, I used Hierarchical partitioning to identify the amount of independent variation explained by each factor when in the presence of the correlated factor.

Beetle species distributions

Of the forty species examined using stepwise GLM, seven species occurred less frequently in more isolated sites (Fig. 2). This pattern was expressed as a higher frequency of

occurrence in Connected or Dense sites (*Chylinus ater*, *Lissotes rodwayi*, Fig. 2A–D), or reduced frequency of occurrence in the small isolated sites (Close, Mid, Distant) (*Decilaus* sp. A, Fig. 2E–F). Four other species had lower frequency of occurrence in Mid and Distant patches compared with all other sites, indicating that distance from large forest patches reduced their frequency of occurrence (Curculionidae species AC and K, *Microchaetes hystricosus*, *Myrmecoholeva acutifrons*, Fig. 2G–J).

Six species occurred more frequently, or were more abundant in the more isolated sites (Fig. 3A–H). *Baeocera* sp. A was absent from Connected sites, but occurred in about 80% of all other sites (Fig. 3A) and *Rybaxis* sp. A showed a similar pattern (Fig. 3B). Pselaphidae sp. I occurred on every Distant, Mid and Close site, but was absent from 30–40% of other landscape elements (Fig. 3C–D). Galerucinae sp. A (Fig. 3E) occurred more frequently, and *Thalycrodes cylindricus* (Fig. 3F) was more abundant in Distant and Mid sites compared with other sites. Galerucinae sp. B occurred more frequently in the small discrete patches (Close, Mid and Distant) than in Connected, Dense or Stream sites (Fig. 3G–H).

Four species had different frequency at intermediate levels of isolation (an interaction). Two species showed highest incidence in Dense (*Sloaneana tasmaniae*, Fig. 4A), or Mid sites (*Metriorhynchus atratus*, Fig. 4B). Two species showed the opposite pattern and were absent from Mid sites (*Heteronyx tasmanicus* and *Tasmanityrus* sp. A, Fig. 4C–D).

Nine species were affected by vegetation factors (Fig. 5A–J). Hierarchical partitioning supported a strong effect of MDS axis 1 or 2 independent of Stream for six of the seven species with significant MDS axes effects (Fig. 5A–D, 5F–H). However, *Tasmanityrus* sp. A showed a strong independent effect of Stream, so the MDS axis 1 effect was mostly due to an affinity of this species for stream-side vegetation (Fig. 5E). Leiodidae sp. A and Phalacridae sp. A showed strong independent effects of Stream where they were less abundant (Fig. 5I–J).

Sixteen species did not have detectable relationships with landscape elements or vegetation MDS axes. None of the significant relationships also had an interaction with Location.

Table 1. R tests (Clarke 1993) comparing differences within and between pairs of landscape elements, based on ranks of Bray-Curtis distances derived from plant species and beetle species data. p -values based on 5000 permutations. p -values <0.05 in bold.

Paired comparison		R (plants)	p (plants)	R (beetles)	p (beetles)
Connected	Close	–0.04	0.643	0.28	0.001
Connected	Dense	0.06	0.255	0.14	0.061
Connected	Distant	0.14	0.030	0.27	0.0002
Connected	Mid	0.19	0.028	0.23	0.011
Connected	Stream	0.51	<0.0002	0.30	<0.0002
Close	Dense	0.04	0.334	0.09	0.164
Close	Distant	–0.06	0.782	0.14	0.024
Close	Mid	0.02	0.434	–0.11	0.846
Close	Stream	0.57	<0.0002	0.43	<0.0002
Dense	Distant	0.13	0.035	0.37	<0.0002
Dense	Mid	0.11	0.128	0.20	0.021
Dense	Stream	0.49	<0.0002	0.27	0.003
Distant	Mid	0.04	0.385	0.23	0.040
Distant	Stream	0.55	<0.0002	0.53	<0.0002
Mid	Stream	0.27	<0.0002	0.21	<0.0002

Fig. 2. Species with reduced frequency of occurrence in more isolated sites. Species names, factor identified in the stepwise GLM and % deviance explained are given for each result. In all cases Other refers to all landscape elements other than those in alternate categories on the figure. Conn = connected. Error bars are 95% CI, and where omitted, the species occurred on all sites of that landscape element.

Dispersal, Presence in the Matrix and Response category

Having wings significantly explained response category (Appendix 1, $F_{1,36} = 7.46$, $p = 0.006$), whereas presence in buttongrass and the interaction of buttongrass and wings did not ($F_{1,36} = 2.4$, 0.11 , $p = 0.37$, 0.54 respectively). Five of six species in response-group inverse could fly, as could 14 of 16 species with no response and six of seven species that were only affected by vegetation. In contrast, two of four species with an interaction could not fly, and five of

seven species that decreased with increasing patch isolation could not fly (Appendix 1).

Metapopulation models

Eight species may not have a metapopulation because they occurred frequently in the matrix (outcome a, see Appendix 1 for all results), although two species also had reduced frequency of occurrence in large or close sites indicating that deterministic processes operate, but not in a metapopulation

Fig. 3. Species with increased frequency of occurrence or increased abundance in more isolated sites. Additional details as for Fig. 2.

context. Three species were very common and widespread (frequency >0.9) and so did not form a metapopulation (outcome b). Four species were absent from medium and distant sites, and were absent or rarely captured in close fragments. These species appear to be extremely poor dispersers and are unable to colonise patches over the buttongrass matrix. They do not form metapopulations among patches (outcome c).

Three species occurred at reduced frequency throughout the patches but at high frequency in Dense or Connected

patches. This pattern is expected for species with a classic metapopulation in a landscape with increasingly isolated patches, but also for species with a mainland-island metapopulation with Connected or Dense sites as a mainland (outcome d).

Thirteen species had distributions consistent with a deterministic metapopulation. Three species may have a deterministic metapopulation based on exclusion from Close, Dense and Connected sites (outcome e). Four species may have a deterministic metapopulation based on

Fig. 4. Species with lower or higher occurrence at intermediate levels of isolation. Additional details as for Fig. 2.

Fig. 5. Species with increased frequency of occurrence or abundance related to differences in Stream or plant community. Results of Hierarchical partitioning included in parentheses (% independent effects for MDSaxis 1, Stream and joint effects, (A–E); MDS axis 2, Stream and joint effects (F–H); Stream, MDS Axis 1, 2 and 3 (joint effects not shown) (I, J). Other details as for Fig. 2. Figures show either the mean and 95% CI for categorical variables, or the predicted relationship and 95% CI for the continuous MDS axis variables. Closed circles on the latter plots are the data points.

higher or lower rates of occurrence in sites of intermediate isolation (outcome f), one of which was also influenced by vegetation. An additional six species may have a deterministic metapopulation based on habitat quality (outcome g). I cannot exclude the possibility that these species may also partly follow a classic metapopulation model because there remained substantial unexplained variation in the stepwise models.

Nine species had no substantial effects in the stepwise models (outcome h), and so may have a classic metapopulation limited by successful establishment, may be widespread but poorly sampled, or may be subject to unmeasured deterministic processes.

Metacommunity models

Predictions of reduced or increased species richness with increased isolation were not observed. The only difference in the number of beetle species was reduced diversity in

Stream sites at Anne and North (Location-Stream interaction $F_{2,52} = 6.59$, $p = 0.002$).

Standard statistical practices cannot be applied to the pair-wise comparisons of Bray-curtis distance because pair-wise comparisons are not all independent. Nevertheless, average distances among landscape elements ranged from 0.61 to 0.74 with large standard deviations, implying there were no significant differences (means (SD) were Connected 0.69 (0.13); Dense 0.71 (0.11); Stream 0.74 (0.15); Close 0.70 (0.13); Mid 0.73 (0.10); Distant 0.61 (0.13)). Therefore, more isolated sites did not have more divergent beetle communities.

Of the thirteen designated rare species, four were in the distance response group indicating they had lower occurrence rates in more isolated patches (Appendix 1). Compared with the 27 other species, three were in response group distance ($p = 0.186$, Fisher's exact test). The Neutral prediction that rare species should decline with increasing isolation is not supported, though this test

may also fail if “rare” species are just infrequently captured and not rare.

To test the Mass-effects prediction of an interaction between isolation and environment, 120 tests of interactions between Isolation 2 and the three MDS axes derived from plant data were made. Six of the tests had $p < 0.05$, which is the same number as expected by chance.

Nested subset analysis

I examined nestedness in six subsets of the data. Species that occurred on three or more sites (105 species), and the 40 abundant species were not significantly nested (% nestedness = 0.51, 3.06, $p = 0.44$, 0.17 respectively). Similarly, species that were significantly affected by vegetation (nine species), and species with no significant effects (16 species) were not nested (% nestedness = 6.3, 2.75, $p = 0.22$, 0.31, respectively). In contrast, species that occurred more frequently in more isolated sites (six species) were strongly nested (% nestedness = 35.12, $p = 0.0012$), as were species that occurred less frequently in more isolated sites (seven species, % nestedness = 41.08, $p = < 0.0002$). Tests using the most isolated subset of data found no significant nesting for the 40 abundant species, nine species with a vegetation effect or 16 species with no effect (% nestedness = -2.4, -10.3, 7.6, $p = 0.70$, 0.85, 0.22 respectively).

Discussion

Metapopulation models

A large proportion of species do not have metapopulations in these fragmented landscapes. From the range of outcomes summarized in Appendix 1, I estimate that at least 15 species (37.5%) but up to 60% of the commonly captured species do not have a metapopulation. Species may not form metapopulations by either having very low dispersal (Driscoll 1997, 1998), by having very high dispersal (Hoole et al. 1999) or by occurring throughout the matrix (Driscoll 2005), and all three patterns were observed among the beetle species in this study. Quintana-Ascencio and Menges (1996) reported that an even higher proportion of plant species (85%) did not form a metapopulation in a naturally patchy rosemary scrub community in Florida. It is possible that in fragmented landscapes, only a proportion of species, even a minority, respond in ways predicted by metapopulation theory.

Interestingly, although the study landscapes closely resemble mainland-island systems, with the small eucalypt patches (islands) surrounded by continuous forest (mainland), only 7.5% of beetle species showed distributions consistent with a mainland-island metapopulation. These species also showed the expected pattern for a classic metapopulation in the study landscapes. Based on empirical research, Harrison and Taylor (1997) argued that some form of a mainland-island structure was more plausible than the classic model. However even this form of metapopulation may be rare because they require a fine

balance between dispersal ability and extinction rate (Harrison and Taylor 1997).

Deterministic metapopulations were probably common, with evidence for deterministic metapopulations in 13 (32.5%) species. Two deterministic processes were involved; one driven by interactions with dispersal limited species, and one affected by habitat quality. Most deterministic metapopulations are driven by habitat condition often associated with plant succession (Thomas et al. 1986, Sjögren-Gulve 1994, Hill et al. 1996), however my study implies that interactions with dispersal limited species may lead to deterministic extinction.

Unexplained variation in the GLMs mean that the nine indeterminate species and the species with deterministic metapopulations may also have some characteristics of classic metapopulations. Therefore, between zero (if the three outcome d species have a mainland-island metapopulation) and 60% of species could operate, at least in part, as a classic metapopulation.

An important caveat is that I could not ascertain the rate of false absences because these data were collected at a single time (Tyre et al. 2003). It is therefore possible that the species I examined were more widespread than I observed, potentially pushing some species towards the patchy populations end of the spectrum and further reducing the proportion of species with some kind of metapopulation dynamics.

Metacommunity models

None of the predictions that were tested for the Neutral or Mass-effects models were supported. The most striking metacommunity pattern was the restriction of poor dispersers to the least isolated sites, and the inverse pattern shown by good dispersers. This led to the nested pattern predicted by the Patch-dynamics model. The mechanism excluding good dispersers from less isolated sites and the identity of excluder species are uncertain. A competition/dispersal tradeoff underlies the development of metacommunity theory (Tilman 1982, Tilman et al. 1994), where species that do not invest in dispersal can invest resources in being better competitors and thereby exclude good dispersers (Stanton et al. 2002). However, other mechanisms may be important, notably predation, parasitism, or a tradeoff between fecundity and dispersal, where highly fecund species can dominate close sites and good dispersers are able to dominate more isolated sites (Kareiva 1990, Holyoak 2000, Yu et al. 2004, Binckley and Resetarits 2005). Therefore, although exclusion of good dispersers by poor dispersers is likely to have occurred, the mechanism of exclusion could be competition, predation, parasitism or differential reproduction rates.

While the Patch-dynamics model is a possible explanation for the inverse distribution pattern, so is the Species-sorting model because the hypothesized predation or competition is confined to a subset of sites. For example, when predatory fish excluded certain pond fauna, Cottenie and De Meester (2004) described it as a Species-sorting process. The Species-sorting model assumes that all species can reach all sites (Leibold et al. 2004, Holyoak et al. 2005), which is only true in the Cottenie and De Meester (2004)

example and this study if the excluder species (poor dispersers) are regarded as part of habitat-condition. The Patch-dynamics and Species-sorting models both, slightly inadequately, describe the same process.

The high or low occurrence rates of four species in Mid sites may involve a combination of dispersal limitation and interaction with species showing an isolation or inverse isolation effect. Lindenmayer et al. (2002) made a similar suggestion to explain higher abundance of some bird species in *Eucalyptus* patches of intermediate size.

Vegetation parameters were the only factors influencing the occurrence of seven mostly flying species. This observation implies that population success is linked to habitat conditions (Species-sorting), or that species differentially colonize patches perceived to be more suitable (Binckley and Resetarits 2005). Presumably habitat specialization permits coexistence with dispersal-limited species because no distance effects were observed. Although the predictions of Mass-effects were not supported, dispersal into sink-habitats remains a possibility because Mass-effects could lead to a weak habitat relationship (Dias 1996, Mouquet and Loreau 2003).

The enormous difference between the buttongrass matrix and *Eucalyptus* scrub beetle communities, despite sample sites being separated by only 20–100 m, strongly supports the Species-sorting model. When contrasting different habitats, it appears that the Species-sorting model describes the most important process.

I have only examined community patterns at one spatial scale and different processes may operate at larger scales. For example, if the main competitive tradeoff is between being winged or not, then widely dispersing species may be competitively equivalent, so that when patches are separated by distances that challenge the dispersal capacity of winged species, community composition may conform more closely to the Neutral model.

Nestedness

Only a subset of beetle species exhibited nested subset patterns, which seems to be typical (Boecklen 1997, Fischer and Lindenmayer 2005, Martinez-Morales 2005). In my study, analysis of isolation effects led to the recognition of two strongly nested groups, which, if examined together, would cancel out each other's nesting pattern. One group showed strong nesting based on limited colonization ability, consistent with established mechanisms of nestedness (Worthen 1996, Wright et al. 1998, Fischer and Lindenmayer 2005). However, the species that increased in frequency of occurrence with isolation have developed nesting through a mechanism that is not frequently discussed in the nested-subset literature, although such mechanisms are thoroughly considered in the metacommunity literature. Likely mechanisms included exclusion by competitors or predators or differential reproduction. This highlights an oversight in the ecological literature to date, where nested subset theory and metacommunity theory are rarely discussed in the same paper (but see Urban 2004), although nestedness is one pattern that can arise through metacommunity processes.

Conclusions

Within the constraints of studying a large scale complex system, I have shown that a large proportion of species may not have a metapopulation and that elements of deterministic metapopulations are likely to predominate. I cannot exclude the possibility that classic metapopulation dynamics are also common in almost two thirds of species, excluding the most dispersal-limited species, the most widely dispersing species and habitat generalists. Among the competing metacommunity models, the data showed that Species-sorting and Patch-dynamics were the most obvious mechanisms leading to community-level patterns.

The inverse-nested pattern highlighted a weakness in current metacommunity models because two models described the same process. One possible solution is a more complex set of terms to expand the four basic models (Leibold et al. 2004, Holyoak et al. 2005). For example, the inverse-nested pattern of this study, and the exclusion of pond fauna by fish (Cottenie and De Meester 2004) are a dispersal-limited Species-sorting process because all species cannot reach all patches. In the dispersal-limited Species-sorting process, the species that cause habitat to be unsuitable for widely dispersing species are confined to certain parts of the landscape due to dispersal limitation. Although the expansion of metacommunity models in this way could lead to a plethora of alternative models and make a-priori predictions under the alternative scenarios cumbersome, it will lead to a theory of metacommunities that is more representative of nature. Alternatively, I have shown that it is also possible to use metapopulation terminology to describe the process as a deterministic metapopulation.

In terms of understanding the study system, metapopulation theory was flexible enough to accommodate all of the spatial patterns with its strong focus on individual species responses. In contrast, some of the tests for metacommunity theory may have failed because they attempt to predict patterns that will only emerge if most species are subject to the same mechanisms. Nevertheless, metacommunity theory seems to be valuable for its emphasis of the key ecological interactions that can lead to spatial patterns, particularly niche specialization and dominant-species – dispersal tradeoffs. However, both of these concepts also have a strong presence in metapopulation theory (Taylor 1990, Thomas 1994, Stelter et al. 1997, Amarasekare and Nisbet 2001, Cronin 2004, Ryall and Fahrig 2006). Perhaps the strength of metacommunity theory will be in describing dynamics in continuous habitat, an area where metapopulation theory does not encroach. The extent of overlap and redundancy in the metacommunity and metapopulation concepts warrant closer scrutiny.

In complex communities with many species it is hard to distinguish among similar competing models, although I have shown that inferences within broad bounds are possible. To better distinguish among models, detailed natural history studies that identify interacting species are needed, followed by experimental studies to test mechanisms of exclusion. However, the value of examining complex communities over simple model systems is that most natural communities are complex. To find out how

important a particular ecological model might be, we must examine how prevalent the proposed mechanisms are in real, usually complex, communities. Understanding which mechanisms are important will be valuable for predicting and ameliorating negative impacts of human-mediated fragmentation on biodiversity, so is a worthy challenge for ecologists.

Acknowledgements – Jenifer Lau, Louise Emmerson and Jemery Day provided valuable feedback on an earlier draft of this paper. Thanks to Jamie Kirkpatrick (plants) and Peter McQuillan (beetles) for assistance with identification and provision of lab facilities. Simon Grove and Marie Yee provided access to Forestry Tasmania's beetle collections. Thanks to Madelaine Hanson for help in the field. This research was completed under Tasmanian Parks and Wildlife Service permit number FA 01030 and was funded through an Australian Research Council Post Doctoral Fellowship, which I held in the School of Geography and Environmental Studies at the Univ. of Tasmania. The project was written up at Flinders Univ. and The Australian National Univ.

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