When log-dwellers meet loggers: impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern Australia

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Abstract

Anthropogenic activities continue to cause massive fragmentation and reduction of forest area worldwide. With fragmentation and reduction of habitat recognized as the greatest threats to biodiversity, the implementation of improved, informed and conservation-based forestry practices is essential, and requires a greater understanding of the responses of different organisms to forest fragmentation. While genetic techniques can add invaluable insights to fragmentation studies they have rarely been employed, particularly for multiple species. In the present study, we combined genetic information, obtained from allozyme loci and anonymous single copy nuclear DNA markers, with ecological data to investigate the impacts of forest fragmentation on two log-dwelling beetles with different life histories, in an 'islands of bush in a sea of pine' model, at Tumut in New South Wales, Australia. Both the relatively mobile (i.e. has high dispersal ability and/or broad habitat range) *Adelium calosomoides* and the less mobile *Apasis puncticeps* showed reduced mobility and gene flow in fragmented compared to continuous forest: there was significantly greater isolation by distance and stronger local structure revealed by spatial autocorrelation in fragmented forest. Analysis of patch and species characteristics revealed that genetic and demographic structure may be influenced by log degradation class for both species, and number of potential dispersal barriers, distance from continuous forest and desiccation intolerance/moisture preference for *Ap. puncticeps*. Thus the pine plantation matrix poses a barrier or filter for gene flow and mobility in both beetle species.

Keywords: Adeliini, allozymes, anonymous nuclear DNA markers, Coleoptera, dispersal, forest fragmentation, gene flow, Lagriinae, mobility, Tenebrionidae

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Introduction

Impacts on biodiversity through loss and fragmentation of forest

Fragmentation and reduction of habitat are recognized as the greatest threats to biodiversity (WCMC 1992), yet anthropogenic practices continue to cause massive fragmentation and reduction of forest area worldwide. At the same time,

there is rapidly accumulating evidence that attendant negative impacts undermine the productivity and sustainability of forestry (Norton 1996; Grove 2002a, b). Thus, the implementation of informed, conservation-based forestry practices has the potential to improve both the long-term viability of forestry and retention of biodiversity.

Forest fragmentation reduces once-continuous areas of forest into smaller, less-connected and isolated remnants, usually receiving fewer migrants and less gene flow. Impeded movement of individuals and their genes have a range of demographic and genetic impacts (Frankham *et al.* 2002), including increased genetic differentiation between populations, reduced genetic variation within populations,

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and altered within-fragment population structures such as the mating system (Frankham *et al.* 2002; Stow & Sunnucks 2004a, b). Reduced migration can impede recolonization of patches operating in a metapopulation structure, and ultimately lead to local or broader extinction (Bradshaw & Marquet 2003).

How fragmentation of forest impacts individual organisms is dependent on the life history attributes of those organisms (Didham *et al.* 1998; Lindenmayer *et al.* 1999; Henle *et al.* 2004; Wiegand *et al.* 2005) and their interaction with a multitude of fragmentation effects, so that only those species that find the new matrix sufficiently hostile may experience impeded migration and gene flow (Berggren *et al.* 2001; Mabry & Barrett 2002). While there have been some extensive programmes on forest vertebrates (e.g. Lindenmayer citations herein; Gibbons *et al.* 2002; Ball *et al.* 2003; Sumner *et al.* 2004), direct information can be difficult to obtain for invertebrates, not least because they are less amenable to capture–mark–recapture. Rapid recent advances in molecular population biology have improved this situation by facilitating highly resolving genetic estimators of mobility and gene flow (Sunnucks 2000; Brouat *et al.* 2003; Keller & Largiadèr 2003). Studies that can estimate migration and gene flow can aid in understanding the complexities of impacts of fragmentation by supplying the missing information about mobility of individuals.

The importance of invertebrates and the saproxylic community

Invertebrates make key contributions to all levels of biodiversity (Erwin 1982; WCMC 1992). Key forest invertebrates include 'saproxylic' organisms, which inhabit decaying wood — the largest pieces of which have been referred to as coarse woody debris (CWD) and diminish through a number of forest management practices (Siitonen 2001; Sippola *et al.* 2001). This resource and its community are now recognized as fundamental to forest function through critical processes such as nutrient cycling (Wallace 1953; Yee *et al.* 2001; Grove *et al.* 2002). We hereafter refer to CWD as fallen timber owing to negative connotations of both 'coarse' and 'debris' used to describe this ecologically critical resource.

Understanding the impacts of habitat alteration on invertebrates that depend on rotting wood and leaf litter is critical. As well as being ecologically (and as a consequence, commercially) important, the saproxylic community contains a disproportionate fraction of species of conservation concern (Yen *et al.* 1990; Grove 2002a). The organisms also have the practical advantages (as models/indicators) of being relatively aseasonal, and distributed in a convenient hierarchy of countable logs in measurable patches within regions.

Experimental approaches to fragmentation: manipulations and pseudo-experiments

Ideally, fragmentation studies should be carried out in manipulation experiments, but for logistic reasons they are rare (Margules 1992; Holt & Debinski 2003). Instead, studies of habitat fragmentation have been largely based on pseudo-experiments, utilizing fragments created through the exploitation of resources (e.g. Niemelä *et al.* 1993; Abensperg-Traun *et al.* 1996; Sumner *et al.* 2004). An important consideration in such studies is the quality and quantity of prefragmentation data. The absence of such data may be compensated for where forest remnants adjoin unfragmented forest representing prefragmented habitat. Buccleuch State Forest (BSF) near Tumut in New South Wales, Australia, meets these requirements, having a large number of eucalypt forest patches in a *Pinus radiata* plantation matrix adjoining large areas of continuous native forest (Lindenmayer 2000).

Studies of the impacts of forest fragmentation have been carried out for a diversity of plant and vertebrate species at BSF (e.g. Lindenmayer 2000 and references within; Lindenmayer & Peakall 2000; Lindenmayer *et al.* 2001a, b; Fischer & Lindenmayer 2002a, b; Gibbons *et al.* 2002; Lindenmayer *et al.* 2002; Ball *et al.* 2003; Banks *et al.* 2005), but there have been no published studies on the effects of habitat fragmentation on invertebrates. Moreover, studies on how fragmentation affects the mobility and gene flow of terrestrial invertebrates are generally lacking globally. A few recent studies have demonstrated significantly altered genetic structure and reduced persistence of populations in fragmented habitats for a range of generalist and specialist as well as high and low gene flow species in recently and historically fragmented systems (Knutsen *et al.* 2000; Brouat *et al.* 2003; Keller & Largiadèr 2003; Williams *et al.* 2003). Together they have shown that genetic responses to fragmentation are species-specific and can be complex, just like the demographic effects with which they are associated (Davies & Margules 1998; Didham *et al.* 1998; Henle *et al.* 2004). Thus, comparative studies and syntheses are needed to formulate useful generalizations (Henle *et al.* 2004).

While genetic techniques can add complementary and novel insights in fragmentation studies (e.g. Stow & Sunnucks 2004a, b and references within), these approaches have rarely been applied in the present context, particularly for multiple species (Brouat *et al.* 2003). In the present study, a combination of genetic and ecological techniques were utilized to examine the effects of forest fragmentation at BSF on the mobility and gene flow of two species of flightless tenebrionid beetles differing in life histories: *Adelium calosomoides* Kirby (1818) and *Apasis puncticeps* Lea (1896). If pine plantation in Australia is hostile to them, *Ap. puncticeps* and *Ad. calosomoides* should display reduced mobility and gene flow among the native forest patches embedded in pine.

Materials and methods

Study site and organisms

Buccleuch State forest (BSF) contains 192 eucalypt forest patches of different size, shape, spatial configuration and fragmentation history, embedded in a 50 000+ ha pine plantation matrix (Lindenmayer 2000). Two tenebrionid beetle species of the subfamily Lagriinae, tribe Adeliini, were collected in a southern section of BSF from patches ranging from 21 to 36 years since their creation, and from adjacent continuous native forest (Fig. 1). *Adelium calosomoides* is the smaller species and occurs largely in dry microhabitats, while we find *Apasis puncticeps* more in moist microhabitats. The different habitat use is consistent with the natural histories of the two genera, from which it might also be inferred that *Adelium* are the more generalist and mobile (Matthews 1998). These beetles are dependent on fallen timber and, being among the major invertebrate consumers of fallen timber at BSF, have the ability to cause physical changes in their environment and influence the availability of resources to other species.

We obtained 2323 adult beetles — 707 *Ap. puncticeps* and 1616 *Ad. calosomoides* — from 142 rotting logs in 52 sites.

Logs were dismantled by hand in March 2001 (sites 25–30, 32–33, 53; Fig. 1), in March 2003 (sites 1–23) and in April–June 2004 (sites 24, 31, 34–51). For each log, GPS coordinates, dimensions, percentage sampled and degradation class (Barclay *et al*. 2000) were recorded. Live specimens were transported to the laboratory and stored at 6 °C, where they were frozen at −80 °C or retained alive for a physiological experiment (below).

Desiccation/heat stress experiment

Beetles were housed for approximately 2 weeks in ventilated containers (r = 7.25 cm, L = 21 cm) containing rotting log material and sliced carrot, then at room temperature (22 °C ± 0.5 °C) for 2 h prior to the experiment. In all, 132 *Ad. calosomoides* and 43 *Ap. puncticeps* were tested for desiccation/heat stress response. Individuals were weighed (accurate to 0.1 mg) and then placed in open containers (r = 2 cm, H = 5.5 cm), which sat in tubs (L = 26 cm, W = 19 cm, H = 10 cm) containing 200 g silica gel desiccant. The tubs were sealed and placed in a 40 °C oven for 2.5 h. Beetles were subsequently weighed, recorded as alive or dead and stored at −80 °C. The experiment was designed following a pilot study (data not shown) that identified the
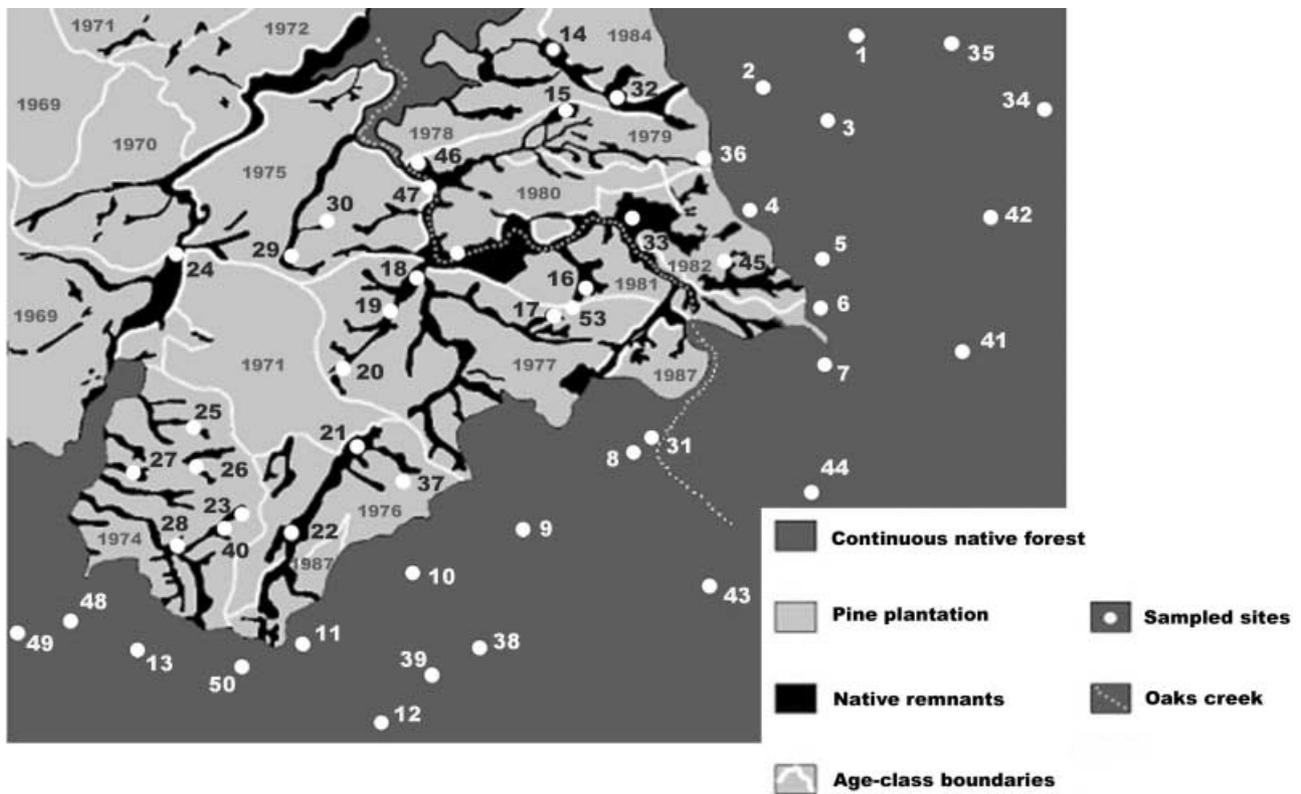

Fig. 1 Location of sampled sites.

narrow range of conditions causing >0% and <100% mortality in both species.

Allozyme electrophoresis and anonymous single-copy nuclear DNA markers

The 23 enzyme systems tested (available upon request) yielded five presumptive polymorphic loci of satisfactory resolution for subsequent population screening: glucose phosphate isomerase (GPI; E.C. 5.3.1.9), phosphogluco-mutase (PGM; E.C. 2.7.5.1), malate dehydrogenase (MDH; E.C. 1.1.1.37), malic enzyme (ME; E.C. 1.1.1.40) and adenylate kinase (AK; E.C. 2.7.4.3) (abbreviations follow Harris & Hopkinson 1976).

Genotypes for each beetle at each locus were determined using cellulose acetate electrophoresis (Titan III system, Helena Laboratories). GPI, PGM, MDH and ME were all resolved using a Tris Glycine buffer of pH 8.0 (Richardson *et al.* 1986) diluted 1:4 with distilled water. GPI and MDH gels were run at 4 °C for 1 h at 200 V, and PGM and ME at room temperature for 35 min at 200 V. AK was resolved using the same buffer diluted 1:2 for 30 min at 4 °C and 200 V. Stain was applied in an agar overlay, and recipes followed Richardson *et al.* (1986) with minor modifications. In all, 1641 beetles (up to 20 per log: 678 *Ap. puncticeps* and 963 *Ad. calosomoides*) were genotyped at the five loci. All those *Ap. puncticeps* were genotyped at single-copy nuclear (scn) DNA loci AP38, A1Mp20U2, S2Gm49 and all *Ad. calosomoides* at AD 19 and AD 32 as per Schmuki *et al.* (in press).

Analysis of genetic data

Whether genetic structure followed a genetic isolation-by-(geographic) distance (IBD) pattern was estimated using Mantel tests (10 000 permutations) in GENEPOP (version 3.4; updated version cf. Raymond & Rousset 1995), based on logarithm of geographic distances and $F_{ST}/(1 - F_{ST})$ (Rousset 1997). Tests for different IBD slopes in continuous and fragmented forest were conducted in POPTOOLS (version 2.5.9; Hood 2003): regression and resample functions were used to generate real and randomized slopes, respectively, and the Monte Carlo function calculated 1000 randomized slope-differences and the number of randomized slopes > the real slope. IBD analyses for sex differences were conducted in the same way.

Spatial autocorrelation analyses were implemented in GENALEX (Peakall & Smouse 2001; version 6.0, Peakall *et al.* 2003) and performed with 9999 permutations for tests of significance, and 999 bootstraps for estimating 95% confidence intervals. Differences in continuous vs. fragmented and male vs. female autocorrelation coefficients (*r*) within distance classes (1000–10 000 m) were assessed relative to 10 000 permuted *r* values; sorted permuted *r* values from

GENALEX were shuffled using the Resample function in POPTOOLS.

Tests for sex-biased dispersal were performed using FSTAT (version 2.9.3.2; Goudet 1995). Allelic richness (using rarefaction to overcome problems associated with uneven sample sizes) and F_{IS} were calculated in FSTAT and observed and expected heterozygosities calculated in POPGENE (version 1.31; Yeh *et al.* 1995).

Uncovering factors contributing to differential dispersal abilities

Two-way analyses of variance (ANOVA) (using the GLM command in SPSS 11.5, SPSS Inc.) were used to test for effects of habitat types (continuous vs. fragmented) on three response variables: allelic richness, F_{IS} and density (all animals sampled per m³ wood at each site; required a third-root transformation to meet the assumptions of ANOVA).

For the fragmented sites, we investigated the effects of three variables (distance of fragmented sites from continuous habitat, number of potential dispersal barriers between fragmented sites and continuous habitat and the area of eucalypt (m²) within a 500-m radius of sampled sites) on densities, allelic richness and F_{IS} of the two beetles using multiple regression. Altitude and fragment age varied little among fragments and were thus excluded from the analysis. Distances from continuous forest were taken as shortest air-line distances. Barriers comprised roads and creeks and were counted if they intersected shortest air-lines between continuous forest and fragmented sites; most were given a value of one barrier, but major gravel roads that were wider and used with high frequency by logging trucks were given a value of two. To avoid patterns of F_{IS} for *Ad. calosomoides* being driven by homozygous excess at AD 19 and AD 32 (Schmuki *et al.* in press), we excluded these loci from this species' data set when examining possible impacts of the three predictor variables (above) on F_{IS}, and for species comparisons of F_{IS}. As explained in Schmuki *et al.* (in press), continuous and fragmented forest sites were equally deficient in heterozygotes at AD 19 and AD 32; we thus found it legitimate to include these loci when comparing the two in other analyses.

To avoid the pitfalls of automated procedures for variable selection (Quinn & Keough 2002), we used model selection based on Akaike's information criterion (AIC, Burnham & Anderson 1998) to evaluate which combination of predictor variables best represented our data. All eight possible additive combinations of predictors (including a 'null' model only containing the intercept) were compared. Each model was fitted with maximum-likelihood estimation of parameters in PROC GENMOD of SAS (SAS Institute 1996) using the identity link and normal errors. From the log-likelihood of each model, AIC_c (AIC adjusted for small sample size) was calculated to identify the most

Table 1 Tests for differences between continuous (C) and fragmented (F) as well as female and male autocorrelation, in 1–10 km distance bins; significantly higher autocorrelation coefficients given in bold

Distance class (m)	*Apasis puncticeps*						*Adelium calosomoides*					
	C	F	*P*	Female	Male	*P*	C	F	*P*	Female	Male	*P*
1000	**0.0489**	0.0398	0.003	**0.0499**	0.0447	0.046	**0.0477**	0.0176	< 0.001	0.0190	**0.0285**	0.002
2000	0.0196	**0.0275**	0.015	0.0080	**0.0245**	< 0.0001	−0.0036	−0.0033	0.661	−0.0004	**0.0086**	0.001
3000	−0.0074	**0.0132**	< 0.0001	0.0075	0.0124	0.058	−0.0158	**−0.0081**	< 0.001	−0.0035	−0.0052	0.513
4000	**0.0117**	0.0008	< 0.001	0.0097	0.0097	0.643	**0.0153**	0.0051	< 0.001	0.0017	0.0010	0.745
5000	**−0.0019**	−0.0159	< 0.0001	−0.0079	**0.0033**	< 0.0001	−0.0018	−0.0007	0.418	0.0027	0.0004	0.311
6000	−0.0178	**−0.0175**	0.660	**0.0003**	−0.0033	0.022	−0.0092	**−0.0053**	0.015	**0.0019**	−0.0027	0.037
7000	**0.0105**	−0.0155	< 0.0001	−0.0064	**−0.0002**	0.029	−0.0087	**0.0052**	< 0.0001	**−0.0010**	−0.0065	0.023
8000	**−0.0012**	−0.0344	< 0.001	−0.0118	**−0.0056**	0.020	**0.0047**	−0.0080	< 0.0001	−0.0054	**−0.0005**	0.002
9000	**−0.0003**	−0.0345	< 0.0001	**−0.0085**	−0.0161	0.004	−0.0005	−0.0029	0.093	−0.0032	**0.0022**	0.003
10 000	**−0.0123**	−0.0434	< 0.001	−0.0188	−0.0189	0.387	N/A	N/A	N/A	−0.0082	**−0.0005**	0.002

parsimonious model (lowest AIC_c), i.e. the one best representing the data using the fewest parameters, properly balancing the errors of over- and underfitting (Burnham & Anderson 1998). Akaike weights were calculated to assess the relative support for each model (Burnham & Anderson 1998). Where model selection provided evidence for a particular predictor to be important, its parameter estimate was obtained by 'model averaging' (Burnham & Anderson 2001), using the estimator of Buckland *et al.* (1997). This method accounts for model selection uncertainty and provides an average across all candidate models containing the predictor, weighted by the relative evidence supporting each model (Burnham & Anderson 2001).

The impact of log degradation class on beetle density was assessed for the combined data set of logs from fragmented and continuous habitat using analysis of covariance (ANCOVA), accounting for the effects of habitat type and site identity.

Results

Number of alleles ranged from two to three, and two to five for *Apasis puncticeps* allozymes and nuclear DNA markers, respectively, and two to six, and eight to ten for *Adelium calosomoides*. Neither species exhibited significant differences in allelic richness or F_{IS} in continuous vs. fragmented forest (two-way ANOVA, $F_{2,83} = 0.12$, $P = 0.89$ and $F_{2,83} = 1.84$, $P = 0.17$, respectively). *Ad. calosomoides* was sampled at significantly ($F_{1,88} = 11.7$, $P < 0.001$) greater densities than *Ap. puncticeps* in both continuous (mean = 2.2 ± 0.21 beetles/m³ wood searched, cf. 1.85 ± 0.21) and fragmented (3.07 ± 0.21 cf. 2.01 ± 0.21) forest, although there is apparently such seasonal variation in the relative abundance of the two species that in some sampling periods many more *Ap. puncticeps* are sampled than *Ad. calosomoides*. *Ap. puncticeps* showed significantly ($P < 0.0001$) stronger patterns of IBD in both forest contexts than did *Ad. calosomoides*

(continuous: b = 0.017 vs. b = −0.00067, $P = 0.014$; fragmented: b = 0.038 vs. b = 0.012, $P < 0.0001$) indicating significantly poorer dispersal ability than *Ad. calosomoides*.

Analyses of spatial genetic structure indicated male-biased dispersal for *Ad. calosomoides*: females displayed significant genetic IBD (b = 0.005, $P = 0.040$), while males did not (b = −0.005, $P = 0.72$). This sex difference was not formally significant ($P = 0.083$) perhaps in part because genetic–geographic relationships in the sexes have different shapes: autocorrelation coefficients (r) were significantly ($P < 0.004$) higher for male *Ad. calosomoides* over the 1000–2000 m and 8000–10 000 m distance classes (Table 1). There were no significant ($P > 0.40$) sex differences in mean assignment index (AIC), variance in AIC, F_{ST}, relatedness, observed heterozygosity (H_O) and gene diversity (H_S).

The same measures revealed no evidence of sex-biased dispersal for *Ap. puncticeps* ($P > 0.20$ for mean AIC, variance AIC, F_{ST}, relatedness, H_O and H_S). The sexes displayed similar, significant IBD (M: b = 0.035, $P < 0.0001$; F: b = 0.032, $P = 0.003$; $P = 0.43$ for the difference) and spatial autocorrelation revealed no consistent sex differences in genotypic structure (Table 1). Since sex differences are slight or absent in both species, data will not be analysed separately by sex below.

Comparison of genotypic structure in continuous and fragmented forest

Adelium calosomoides. A strong significant pattern of genetic IBD was found for this species in fragmented forest (b = 0.012, $P = 0.0007$), but there was no sign of genetic differentiation with distance in the continuous forest (b = −0.00067, $P = 0.46$). Regression slopes for the two forest contexts differed significantly ($P = 0.002$, permuted differences in slopes). Spatial autocorrelograms showed similar genotypic structure in both forest contexts (Fig. 2),
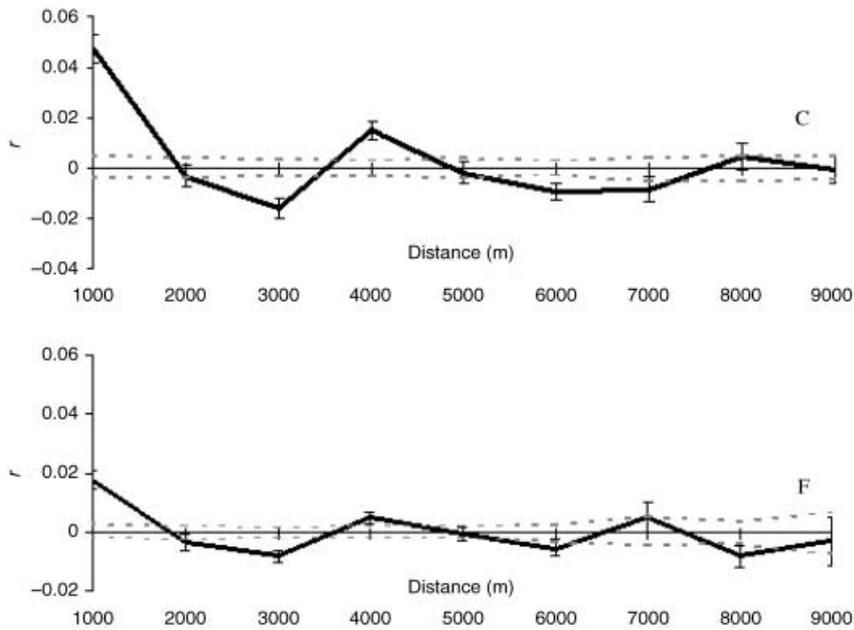
Fig. 2 Spatial autocorrelograms for *Adelium calosomoides* in continuous (C) and fragmented (F) forest: black solid lines, autocorrelation coefficient (*r*); grey broken lines, upper and lower confidence.
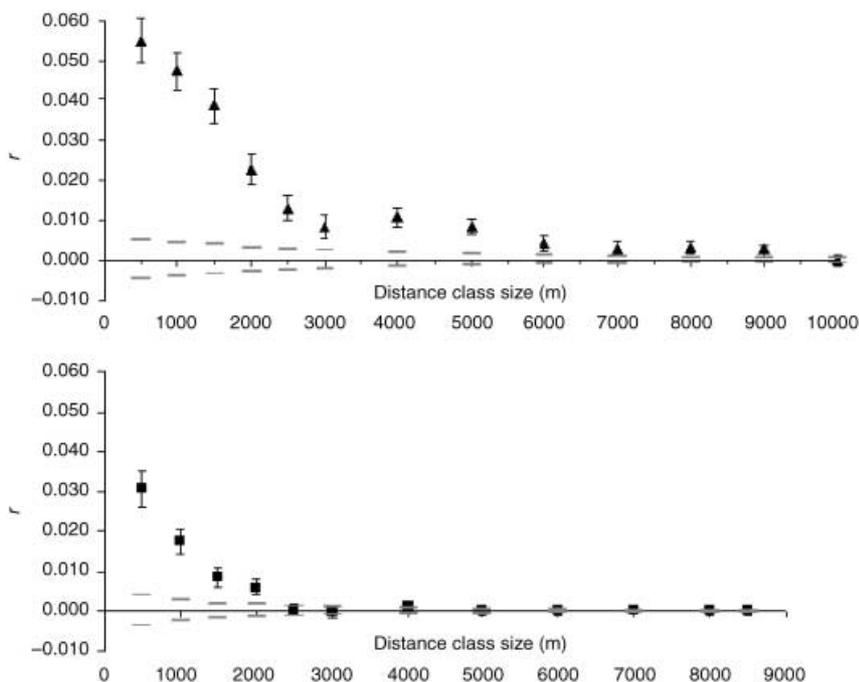

Fig. 3 Autocorrelation for increasing distance-class sizes in continuous (▲) compared to fragmented (■) forest for *Ad. calosomoides*: black shapes, autocorrelation coefficient (obtained from 1st distance bins only); grey lines, upper and lower confidence.

with oscillation of positive and negative autocorrelation across both continuous and fragmented forest, but genotypes were significantly more similar over shorter distances in the continuous forest than in the fragmented one (continuous: *r* = 0.048; fragmented: *r* = 0.016; *P* = 0.0001). The difference in genetic structure in the two forest types can be seen more easily by examination of the outcomes of the Peakall *et al*. technique (2003) of iteratively increasing

distance bins and plotting *r* only for the first bin in each case — this approach revealed positive structure up to 9.0 km in continuous forest compared to only 2.0 km in fragmented forest (Fig. 3).

Apasis puncticeps. A pattern of genetic IBD was revealed for *Ap. puncticeps* in both continuous and fragmented forest (*P* = 0.003 and *P* < 0.0001, respectively), but the IBD
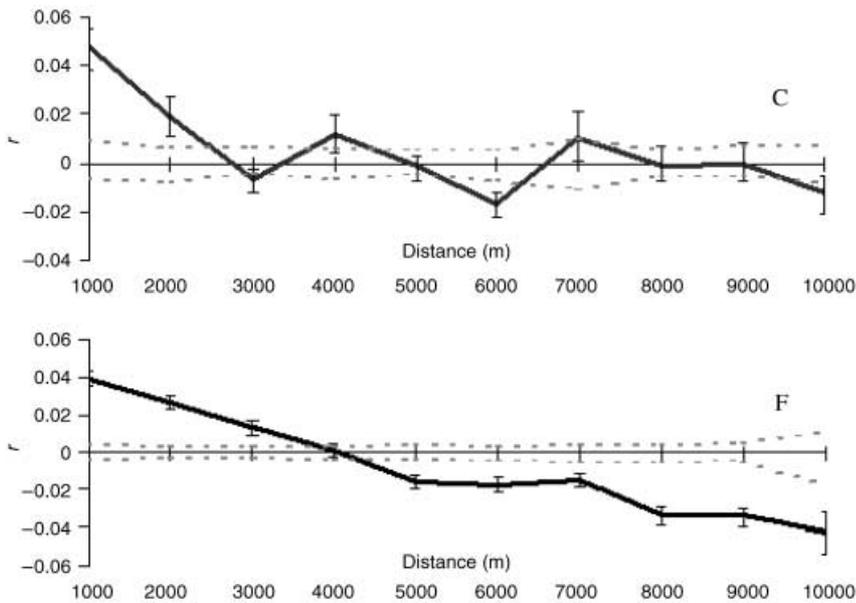
Fig. 4 Spatial autocorrelograms for *Apasis puncticeps* in continuous (C) and fragmented (F) forest: black solid lines, autocorrelation coefficient (*r*); grey broken lines, upper and lower confidence.

regression slope for fragmented forest was significantly steeper than that for continuous forest (b = 0.038 cf. 0.017; *P* = 0.004 by permuting differences in slopes). Consistent with this, autocorrelograms for *Ap. puncticeps* showed positively autocorrelated genotypes over short geographic distance classes in both forest contexts, but there was a strong pattern of genotypic dissimilarity with distance in the fragmented forest compared to the continuous forest, which showed oscillation of positive and negative auto-correlations (Fig. 4). Tests for differences in continuous- and fragmented-forest autocorrelation coefficients (*r*) for distance classes 1000–9000 m were performed by permuta-tion. In fragmented forest, positive structure was signi-ficantly lower over the smallest (up to 1000 m) and largest distances (4000–5000 m, 7000–10 000 m) and significantly higher over intermediate ones (2000–3000 m) (Table 1). This nonlinear pattern could be generated by dispersers necessarily undergoing atypically long dispersal to the next patch, with increased habitat 'viscosity' over long distances.

Contributions to reduced mobility and gene flow in fragmented forest

Patch and habitat characteristics. Species-specific patterns were seen for variation in each of allelic richness, F_{IS} and beetle density. Model selection showed that allelic richness of *Ap. puncticeps* was mainly affected by distance from continuous forest, since the regression model best sup-ported by the data was one containing the intercept and distance from continuous forest as the only explanatory variable. This conclusion is further supported by the fact

that the combined Akaike weights of all models containing this variable amount to 0.966, leaving very little support for any model without that variable. Model averaging estimated an increase in allelic richness of 0.113 ± 0.035 for every kilometre from continuous forest (Table 2). In *Ad. calosomoides*, none of the environmental variables had much effect on allelic richness. The best regression model contained the intercept and area of eucalypt, but was only marginally better supported than the 'null model' containing the intercept alone (Table 2).

In *Ap. puncticeps*, F_{IS} for a patch increased with the number of potential dispersal barriers between a fragment and the continuous forest. The model containing the number of barriers as the only predictor was best supported and the combined Akaike weight of all models containing this predictor was 0.716. Model averaging estimated an increase in F_{IS} of 0.025 ± 0.013 for each additional barrier. In *Ad. calosomoides*, none of the patch characteristics appeared to affect F_{IS} (Table 2).

Density of *Ap. puncticeps* in fragments was also impacted by the number of potential dispersal barriers from contin-uous forest, declining by 0.225 ± 0.092 with each additional barrier (model-averaged estimate). The regression model only containing this predictor was by far the most parsimo-nious and the combined Akaike weights of models con-taining barriers amounted to 0.963 (Table 2). Density of *Ad. calosomoides* was not strongly influenced by any of the three predictor variables (Table 2).

Analysis of log degradation class showed that beetles of both species occurred at higher densities in less decomposed logs (*Ap. puncticeps*: *P* < 0.001; *Ad. calosomoides*: *P* = 0.011, ANCOVA, accounting for the effects of habitat type and

Table 2 Multiple regression and model selection results using the following predictor variables: distance (m) from continuous forest (dist), number of potential barriers between continuous forest and sampled site (barr) and area of eucalypt within 0.5 km surrounding sites (euc05). The best explanatory model in each case is given in bold: *italics*, positive effect; <u>underlined</u>, negative effect. AIC_c, Akaike information criterion corrected for small sample size; delta AIC_c, the difference in AIC_c between the model under consideration and the most parsimonious one

Model	*Apasis puncticeps*						*Adelium calosomoides*					
	Density		Allelic richness		F_{IS}		Density		Allelic richness		F_{IS}	
	Delta AIC_c	Akaike weight	Delta AIC_c	Akaike weight	Delta AIC_c	Akaike weight	Delta AIC_c	Akaike weight	Delta AIC_c	Akaike weight	Delta AIC_c	Akaike weight
c	9.070	0.006	7.235	0.012	2.174	0.102	***0.000***	***0.452***	0.361	0.226	***0.000***	***0.321***
c + dist	8.169	0.009	***0.000***	***0.455***	4.686	0.029	2.407	0.136	2.283	0.086	0.215	0.289
c + barr	**<u>0.000</u>**	**<u>0.551</u>**	9.065	0.005	***0.000***	***0.304***	2.158	0.154	0.888	0.174	2.483	0.093
c + euc05	8.334	0.009	7.264	0.012	1.841	0.121	2.425	0.134	***0.000***	***0.271***	2.460	0.094
c + dist + barr	2.252	0.179	2.152	0.155	2.842	0.073	4.854	0.040	3.616	0.044	2.644	0.086
c + dist + euc05	7.565	0.013	1.088	0.264	4.520	0.032	5.104	0.035	2.460	0.079	2.873	0.076
c + barr + euc05	2.245	0.179	8.936	0.005	0.148	0.282	4.837	0.040	2.030	0.098	5.245	0.023
c + dist + barr + euc05	4.635	0.054	3.203	0.092	3.337	0.057	7.847	0.009	5.114	0.021	5.784	0.018

site). Highest densities occurred in logs of degradation class 2.

Species desiccation/heat shock tolerance. Approximately equal proportions of body weight were lost by each species during the dry heat treatment (Fig. 4), but the effects were profoundly different. Of 134 *Ad. calosomoides* desiccated, 125 (93.3%) remained alive throughout the experiment, compared with only 9 of 41 (22%) *Ap. puncticeps* ($\chi^2 = 82.6$, d.f. = 1, $P < 0.0001$). Thus the prediction that *Ap. puncticeps* should be less tolerant than *Ad. calosomoides* of hot/dry conditions was validated.

For a summary of the main characteristics of and findings for each organism, see Table 3.

Discussion

There is a growing catalogue of measurable impacts of forest fragmentation on organisms, based on demographic and ecological information (e.g. Margules *et al.* 1994; Davies *et al.* 2000; Grove 2002a). Increasingly the same can be said for genetic data (e.g. Knutsen *et al.* 2000; Brouat *et al.* 2003; Keller & Largiadèr 2003). While our focus is on saproxylic (dead-wood dependent) invertebrates, larger and potentially more mobile species can be impacted by habitat disruption. For example, in as few as 10 generations, prickly forest skinks (*Gnypetoscincus queenslandiae*) displayed disruption of gene flow in fragmented forest (Sumner *et al.* 2004). Even organisms that occupy naturally patchy habitat may rapidly show measurable genetic signals of reduced dispersal and gene flow, in the face of removal of natural vegetation (e.g. Cunningham's skink *Egernia cunninghami*, Stow *et al.* 2001; Stow & Sunnucks 2004a, b).

To the list of species that show impacts of forest fragmentation, we can now add two wood-boring, flightless tenebrionid beetles in Australian eucalypt forest, fragmented in the previous 21–36 years. The species differences reported here reiterate that the impacts of fragmentation interact with the ecology and biology of the species (Schiegg 2000a, b; Kattan & Murcia 2003). Notwithstanding idiosyncratic responses, *Apasis puncticeps* and *Adelium calosomoides* both showed evidence of decreased mobility in the face of replacement of natural forest with plantations of pine. This potentially negative impact is consistent with the results of the majority of ecological studies on saproxylic beetles and other forest organisms (references in the Introduction; Cunningham & Moritz 1998; Zanette *et al.* 2000).

Population genetic structure in continuous native forest

Adelium calosomoides showed very little genetic structuring in continuous forest over the spatial scale of ~10 km represented in the samples: little to no genetic differentiation with distance and positive structure up to 9 km as shown by spatial autocorrelation both agreed. As predicted from natural history, *Ap. puncticeps* showed a more genetically localized structure, which may be due to the apparent preference for or limitation to moister microhabitat. Such microhabitats are relatively rare through a large proportion of BSF. The inferred differences in localization of population structure of the present two target species is consistent with the findings for a large number of organisms, including forest-dwelling carabid beetles, in which habitat specialists (for whom habitat is naturally relatively fragmented) tend to be more strongly structured than generalists (Brouat *et al.* 2003).

Table 3 Summary of the main characteristics of- and findings for *Apsis puncticeps* and *Adeliium calosomoides*; C, continuous forest; F, fragmented forest

		Apasis puncticeps		*Adelium calosomoides*	
Habitat preference		Moist		Dry	
Dispersal ability		Lower		Higher	
Densities		Lower		Higher	
Isolation by distance (IBD)?		C	F	C	F
		3	3	✗	✓
IBD greater in F?		✓ $P = 0.004$		✓ $P = 0.002$	
Spatial autocorrelation		• Strong pattern of genotypic dissimilarity with distance in F but not C		Positive structure up to 9 km in C vs. 2 km in F	
		• Autocorrelation (r) in F significantly lower than in C over smallest (up to 1000 m) and largest (7000–10 000 m) distance classes			
Patch factors that explain patterning of variables (positive/negative effect)	F_{IS}	Number of barriers (+)		None	
	Allelic richness	Distance from C (+)		Area (m²) of surrounding eucalypt within 0.5 km (+)	
	Density	Number of barriers (–)		None	

Reduced mobility and gene flow through the pine matrix

Both *Ap. puncticeps* and *Ad. calosomoides* showed evidence of reduced mobility and gene flow in fragmented compared to continuous forest, including significantly greater IBD, significantly stronger local structure in spatial autocorrelation, and significant patterning of F_{IS}, allelic richness and density (see below). It is perhaps surprising that common and robust insects could be measurably impacted after 21–36 years of habitat modification. This is likely to represent only in the order of 10 or 15 generations — although their life cycle is very poorly known (E. Matthews, personal communication), many saproxylic beetles have extended life cycles, e.g. the fungivorous beetle *Bolitophagus reticulatus* is inferred to have a 2-year development cycle (Knutsen *et al.* 2000). Such a life cycle is likely to apply in the present cases: the species are large and live at generally low temperatures, feeding on decaying wood.

The observed spatial genetic patterns imply that the pine plantation matrix for both beetle species poses a barrier or filter to gene flow and mobility. A major reason that pine plantation is likely to impede mobility is its low levels of leaf litter and mature fallen timber. These materials are relatively rare even in mature pine stands, but essentially absent for some years after initial clearance of native forest and burning of residue, or after harvesting of pine and planting of subsequent rotations. Other factors may also contribute to the pine matrix presenting a barrier: tree genus, diameter of fallen timber and temporal continuity of fallen timber have all shown to be key factors in saproxylic beetle richness and community composition (Grove *et al.* 2002).

We predicted fragmentation of forest to have a considerably greater impact on the less-mobile *Ap. puncticeps* than

the more desiccation-tolerant *Ad. calosomoides* (that difference being validated here for the first time, albeit by a fairly crude desiccation/heat tolerance experiment), and this was indeed the case. While *Ad. calosomoides* showed consistently higher autocorrelation of genotypes in continuous compared to fragmented forest over most distance classes, it was *Ap. puncticeps* that showed consistent significant negative spatial autocorrelation over the intermediate and larger distances in fragmented but not continuous forest. The F_{IS}, AR and density analyses are relevant here, but are discussed below since they involve impacts of habitat factors.

Predictors of genetic diversity and population density

In the current data set, we detected statistically significant effects of distance from continuous forest and number of barriers (creeks and roads) on *Ap. puncticeps* allelic richness, density and F_{IS}. Related studies have shown creeks, streams and roads to be strong barriers to gene flow (e.g. in carabid beetles) and reduced genetic variation for a range of different taxa in fragments compared to continuous areas have been reported (e.g. Kane *et al.* 1992; Keller & Largiadèr 2003; Williams *et al.* 2003; Wilson & Provan 2003). Similarly, creeks and roads featured in well-supported multiple regression models that explain patterns of F_{IS} and density in *Ap. puncticeps.*

Increased number of potential barriers was accompanied by reduced density and increased F_{IS} within sites for *Ap. puncticeps*. This pattern of F_{IS} might be explained if more-isolated fragments receive fewer migrants, favouring stochastic deviations from panmixia by initial founder effect and preservation of transient family structure. The

F_{IS} pattern would also be promoted if *Ap. puncticeps* naturally disperse for distances greater than roads and/or creeks, acting as barriers, allow (this would maintain the stochastic impact and would slow panmixia) or alternatively if inbreeding avoidance is naturally driven by dispersal (rather than by, e.g. kin recognition), and inbreeding occurs as a consequence of impeded dispersal (Stow & Sunnucks 2004b and references). While the finding of increased allelic richness further from continuous forest is potentially surprising at first, it is consistent with the pattern in F_{IS} if it reflects local genetic drift wherein more isolated units, farthest from continuous habitat, retain different alleles by chance and less isolated units, closer to continuous habitat, are less amenable to genetic drift (analogous with the higher retention of allelic diversity in 'several small' captive breeding designs than 'single large' ones; Frankham *et al.* 2002). Reduced density of *Ap. puncticeps* with increased number of barriers integrates well with a range of related studies demonstrating declines in species richness and relative abundance accompanying habitat modification and isolation, particularly for species of low mobility and/or high habitat specificity (see, e.g. Davies *et al.* 2000; Thomas 2000; Rainio & Niemelä 2003). In a specific example, the density of roads significantly reduced the occupation probability of ponds by the moor frog *Rana arvalis* (Vos & Chardon 1998).

Adelium calosomoides showed significantly elevated densities in fragmented forest, but not with number of barriers, distance from continuous forest or area of surrounding eucalypt within 500 m. Increased population density after fragmentation are not unusual for forest beetles, but may be artefactual and transitory, for example given the decay of habitat logs that may not be replaced in altered forests (Grove 2002b). Indeed for both species, densities were highest in logs of decay class 2, which reflects field observations that larvae and adults of both species consume hard wood and adults prefer to shelter in structurally strong galleries in logs with existing but fractured outer layers.

The associations detected between number of barriers and *Ap. punticeps* density and heterozygosity indicate that populations of this species may be further fragmented by increased number of (access) roads usually associated with plantation forests. That density and patterns of F_{IS} and/or allelic richness for *Ad. calosomoides* were apparently not impacted by roads and/or creeks is likely due to this species being the better disperser and therefore less impacted by fragmentation of forest. Beetles may be forced to travel greater distances in fragmented forest for suitable logs or habitat patches, which would further differentiate impacts on efficient vs. limited dispersers. The slight male-biased dispersal detected for *Ad. calosmoides* may also increase dispersal of this species relative to *Ap. puncticeps* if the process is not disrupted by fragmentation and *Ad. calosomoides* males have to travel further for suitable mates. Despite its dispersal ability, *Ad. calosomoides* nonetheless showed detectably impeded mobility through patch-and-pine matrix relative to adjacent continuous forest.

Concluding remarks

Spatial analysis of genetic data was able to detect significant impacts on mobility and gene flow in each species even with a relatively weak genetic assay. We take this as an indication of the value of molecular population genetic approaches in detecting impacts of human activities on natural population structures, perhaps in advance of serious ecological and evolutionary adverse effects (see also Stow & Sunnucks 2004a, b). Spatial and genetic data together were able to detect evidence of modest sex-biased dispersal, where genetic data alone did not, highlighting the value of analysing spatial information in population genetic patterning.

In the current analyses, *Ad. calosomoides* was found to be a much better disperser than was *Ap. puncticeps.* Both showed significant signals of inhibition of mobility and gene flow in only 21–36 years. While natural habitat removal at BSF has been extensive, there are still substantial networks of riparian vegetation, and a generally high level of connectivity of remnant vegetation (Fig. 1). Thus, the impacts we have detected do not bode well for invertebrates of equal or lesser mobility than the present species in equally or more disturbed environments. As well as the potential for changing genetic structures and altering microevolutionary processes, reduced dispersal is likely to decrease the probability of and/or increase the time to recolonization of patches that have suffered stochastic extinction. It should not be assumed that such impacts will not affect species of appreciable mobility such as those studied here: life histories of mobile animals may be geared to require high levels of gene flow to maintain variation and adaptive and evolutionary potential (Waples 1998).

References

Abensperg-Traun M, Smith GT, Arnold GW, Steven DE (1996) The effects of habitat fragmentation and livestock grazing on animal

communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheat belt. I. Arthropods. *Journal of Applied Ecology*, **33**, 1281–1301.

Ball SJ, Lindenmayer BD, Possingham HP (2003) The predictive accuracy of population viability analysis: a test using data from two small mammal species in a fragmented landscape. *Biodiversity and Conservation*, **12**, 2393–2413.

Banks SC, Finlayson GR, Lawson SJ *et al.* (2005) The effects of habitat fragmentation due to forestry plantation establishment on demography and genetic variation in a marsupial carnivore, *Antechinus agilis*. *Biological Conservation*, **122**, 581–597.

Barclay S, Ash JE, Rowell DM (2000) Environmental factors influencing the presence and abundance of a log-dwelling invertebrate, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). *Journal of Zoology*, **250**, 425–436.

Berggren A, Carlson A, Kindvall O (2001) The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets *Metrioptera roeseli*. *Journal of Animal Ecology*, **70**, 663–670.

Bradshaw GA, Marquet PA (2003) How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas (eds Bradshaw GA, Marquet PA), pp. 1–353. Springer-Verlag, Berlin.

Brouat C, Sennedot F, Audiot P, Leblois R, Rasplus JY (2003) Fine-scale genetic structure of two carabid species with contrasted levels of habitat specialization. *Molecular Ecology*, **12**, 1731–1745.

Buckland ST, Burnham KP, Augustin NH (1997) Model selection: an integral part of inference. *Biometrics*, **53**, 603–618.

Burnham KPA, Anderson DR (1998) *Model Selection and Inference.* Springer, New York.

Burnham KPA, Anderson DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, **28**, 111–119.

Cunningham M, Moritz C (1998) Genetic effects of forest fragmentation on a rainforest restricted lizard (Scincidae, *Gnypetoscincus queenslandiae*).

Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles — experimental evidence. *Journal of Animal Ecology*, **67**, 460–471.

Davies KE, Margules CR, Lawrence JE (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**, 1450–1461.

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998) Beetle species responses to tropical forest fragmentation. *Ecological Monographs*, **68**, 295–323.

Erwin TL (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin*, **36**, 74–75.

Fischer J, Lindenmayer DB (2002a) The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 1. Species composition and site occupancy patterns. *Biodiversity and Conservation*, **11**, 807–832.

Fischer J, Lindenmayer DB (2002b) Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. *Biological Conservation*, **106**, 129–136.

Frankham R, Ballou JD, Briscoe DA (2002) *Introduction to Conservation Genetics.* Cambridge University Press, Cambridge, UK.

Gibbons P, Lindenmayer DB, Barry SC, Tanton MT (2002) Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biological Conservation*, **103**, 1–12.

Goudet J (1995) FSTAT version 1.2: a computer program to calculate *F*-statistics. *Journal of Heredity*, **86**, 485–486.

Grove SJ (2002a) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation*, **104**, 149–171.

Grove SJ (2002b) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1–23.

Grove S, Meggs J, Goodwin A (2002) *A Review of Biodiversity Conservation Issues Relating to Coarse Woody Debris Management in the Wet Eucalypt Production Forests of Tasmania.* Division of Forest Research and Development, Division of Forest Management, Hobart.

Harris H, Hopkinson DA (1976) *Handbook of Enzyme Electrophoresis in Human Genetics.* Elsevier, New York.

Henle K, Davies K, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.

Holt RD, Debinski DM (2003) Reflections on landscape experiments and ecological theory: tools for the study of habitat fragmentation. In: *How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas* (eds Bradshaw GA, Marquet PA), pp. 201–223. Springer-Verlag, Berlin.

Hood G (2003) POPTOOLS. CSIRO, Canberra, Australia.

Kane TC, Barr TCJ, Badaracca WJ (1992) Cave beetle genetics geology and geneflow. *Heredity*, **68**, 277–286.

Kattan GH, Murcia C (2003) A review and synthesis of conceptual frameworks for the study of forest fragmentation. In: *How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas* (eds Bradshaw GA, Marquet PA), pp. 183–200. Springer-Verlag, Berlin.

Keller I, Largiadèr CR (2003) Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **270**, 417–423.

Kirby W (1818) A century of insects, including several new genera described from his cabinet. *Transactions of the Linnean Society of London*, **12**, 375–453.

Knutsen H, Rukke BA, Jorde PE, Ims RA (2000) Genetic differentiation among populations of the beetle *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae) in a fragmented and a continuous landscape. *Heredity*, **84**, 667–676.

Lea AM (1896) Descriptions of new species of Australian Coleoptera. *Proceedings of the Linnean Society of New South Wales*, 284–319.

Lindenmayer BD (2000) *Islands of bush in a sea of pines: a summary of studies from the Tumut fragmentation experiment.* National Research and Development Program on Rehabilitation, Management and Conservation of Remnant Vegetation, Research Report, Australian National University, Canberra, Australia.

Lindenmayer D, Peakall R (2000) The Tumut experiment — integrating demographic and genetic studies to unravel fragmentation effects: a case study of the native bush rat. *Genetics, Demography and Viability of Fragmented Populations*, **4**, 173–201.

Lindenmayer DB, Cunningham RB, Pope ML (1999) A large-scale 'experiment' to examine the effects of landscape context and habitat fragmentation on mammals. *Biological Conservation*, **88**, 387–403.

Lindenmayer DB, Ball I, Possingham HP, McCarthy MA, Pope ML (2001a) A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis. *Journal of Applied Ecology*, **38**, 36–48.

Lindenmayer DB, McCarthy MA, Possingham HP, Legg S (2001b) A simple landscape-scale test of a spatially explicit population model: patch occupancy in fragmented south-eastern Australian forests. *Oikos*, **92**, 445–458.

Lindenmayer DB, Cunningham RB, Donnelly CF, Nix H, Lindenmayer BD (2002) Effects of forest fragmentation on bird assemblages in a novel landscape context. *Ecological Monographs*, **72**, 1–18.

Mabry KE, Barrett GW (2002) Effects of corridors on home range sizes and interpatch movements of three small mammal species. *Landscape Ecology*, **17**, 629–636.

Margules C (1992) The Wog Wog habitat fragmentation experiment. *Environmental Conservation*, **19**, 316–325.

Margules CR, Milkovits GA, Smith GT (1994) Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. *Ecology*, **75**, 2033–2042.

Matthews EG (1998) Classification, phylogeny and biogeography of the genera of Adeliini (coleoptera, tenebrionidae). *Invertebrate Taxonomy*, **12**, 685–824.

Niemelä J, Langor D, Spence JR (1993) Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera, Carabidae) in western Canada. *Conservation Biology*, **7**, 551–561.

Norton TW (1996) Conserving biological diversity in Australia's temperate eucalypt forests. *Forest Ecology and Management*, **85**, 21–33.

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, **57**, 1182–1195.

Peakall R, Smouse PE (2001) GENALEX Version 5: Genetic Analysis in Excel. Population genetic software for teaching and research. Australian National University, Canberra, Australia.

Quinn GP, Keough MJ (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.

Rainio J, Niemelä J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, **12**, 487–506.

Raymond M, Rousset F (1995) GENEPOP (version 1.2): a population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Richardson BJ, Baverstock PR, Adams M (1986) *Allozyme Electrophoresis: A Handbook for Animal Systematics and Population Studies*. Academic Press, San Diego, California.

Rousset F (1997) Genetic differentiation and estimation of gene flow from f-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

SAS Institute (1996) SAS/STAT Software: Changes and Enhancements Through Release 6.11. SAS Institute, Cary, North Carolina.

Schiegg K (2000a) Are there saproxylic beetle species characteristic of high dead wood connectivity? *Ecography*, **23**, 579–587.

Schiegg K (2000b) Effects of dead wood Volume and connectivity on saproxylic insect species diversity. *Ecoscience*, **7**, 290–298.

Schmuki C, Blacket MJ, Sunnucks P (in press) Anonymous scnDNA markers for two endemic log-dwelling beetles: *Apasis puncticeps* and *Adelium calosomoides* (Tenebrionidae: Lagriinae: Adeliini). *Molecular Ecology Notes*.

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, **49**, 11–41.

Sippola AL, Lehesvirta T, Renvall P (2001) Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. *Ecological Bulletins*, **49**, 243–254.

Stow AJ, Sunnucks P (2004a) High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology*, **13**, 419–430.

Stow AJ, Sunnucks P (2004b) Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology*, **13**, 443–447.

Stow AJ, Sunnucks P, Briscoe DA, Gardener MG (2001) The impact of habitat fragmentation on dispersal in Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology*, **10**, 867–878.

Sumner J, Jessop T, Paetkau D, Moritz C (2004) Limited effect of anthropogenic habitat fragmentation on molecular diversity in a rainforest skink, *Gnypetoscincus queenslandiae*. *Molecular Ecology*, **13**, 259–269.

Sunnucks P (2000) Efficient genetic markers for population biology. *Trends in Ecology & Evolution*, **15**, 199–203.

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **267**, 139–145.

Vos CC, Chardon JP (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology*, **35**, 44–56.

Wallace HR (1953) The ecology of the insect fauna of pine stumps. *Journal of Animal Ecology*, **22**, 154–169.

Waples RS (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, **89**, 438–450.

Wiegand T, Revilla E, Moloney KA (2005) Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology*, **19**, 108–121.

Williams BL, Brawn JD, Paige KN (2003) Landscape scale genetic effects of habitat fragmentation on a high gene flow species: *Speyeria idalia* (Nymphalidae). *Molecular Ecology*, **12**, 11–20.

Wilson PJ, Provan J (2003) Effect of habitat fragmentation on levels and patterns of genetic diversity in natural populations of the peat moss Polytrichum commune. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **270**, 881–886.

World Conservation Monitoring Centre (WCMC) (1992) *Global Biodiversity: Status of the Earth's Living Resources*. Chapman & Hall, London.

Yee M, Yuan ZQ, Mohammed C (2001) Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. *Tasforests*, **13**, 119–128.

Yeh F, Yang RC, Boyle T (1995) POPGENE, the user-friendly shareware for population genetic analysis. *Molecular Biology and Biotechnology Centre*. University of Alberta, Edmonton, Canada.

Yen AL, New TR, Van Praagh BD, Vaughan PJ (1990) Invertebrate conservation: three case studies in south-eastern Australia. In: *Management and Conservation of Small Populations* (eds Clark TW, Seebeck JH). Chicago Zoological Society, Chicago.

Zanette L, Doyle P, Tremont SM (2000) Food shortage in small fragments: Evidence from an area-sensitive passerine. *Ecology*, **81**, 1654–1666.