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Anthropogenic landscape change promotes asymmetric dispersal and limits regional patch occupancy in a spatially structured bird population

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Running title: Landscape change, occupancy and asymmetric dispersal

1 **Summary**

- 2 1. Local extinction of habitat patches and asymmetric dispersal between patches are key
3 processes structuring animal populations in heterogeneous environments. Effective landscape
4 conservation requires an understanding of how habitat loss and fragmentation influence
5 demographic processes within populations and movement between populations.
- 6 2. We used patch occupancy surveys and molecular data for a rainforest bird, the logrunner
7 (*Orthonyx temminckii*), to determine 1) the effects of landscape change and patch structure on
8 local extinction, 2) the degree of asymmetry of emigration and immigration rates, 3) the relative
9 influence of local and between-population landscapes on asymmetric emigration and
10 immigration, and 4) the relative contributions of habitat loss and habitat fragmentation to
11 asymmetric emigration and immigration.
- 12 3. Whether or not a patch was occupied by logrunners was primarily determined by the isolation
13 of that patch. After controlling for patch isolation, patch occupancy declined in landscapes
14 experiencing high levels of rainforest loss over time. Processes of habitat loss and fragmentation
15 over time influenced logrunner occupancy over and above the current pattern of patch isolation.
- 16 4. We discovered a high degree of asymmetric dispersal between logrunner populations. The
17 capacity of landscapes to produce surplus emigrants that reproduced in other populations was
18 lower in fragmented local landscapes, but emigration was not limited by the structure of the
19 intervening landscapes. In contrast, the arrival of immigrant logrunners was greater in
20 fragmented local landscapes and was lower when the between-population landscapes were
21 fragmented. Rainforest fragmentation influenced asymmetric dispersal to a greater extent than
22 rainforest loss and a 60% reduction in patch size was capable of switching a population from
23 being a net exporter to a net importer of dispersing logrunners.

1 5. The synergistic effects of landscape change on species occurrence and asymmetric dispersal
2 have important implications for conservation. Conservation measures that maintain large patch
3 sizes in the landscape may promote asymmetric dispersal from intact to fragmented landscapes
4 and allow rainforest bird populations to persist in fragmented and degraded landscapes. These
5 sink populations could form the kernel of source populations given sufficient habitat restoration.
6 However, the success of this rescue effect will depend on the quality of intervening landscapes.

7

8 Key words: asymmetric migration, asymmetric gene flow, bird conservation, detection
9 probability, dispersal asymmetry, coalescent theory, landscape ecology, landscape genetics,
10 microsatellite DNA, subtropical rainforest.

11

12 **Introduction**

13 The local extinction of habitat patches and dispersal between the patches are key
14 processes structuring animal populations in heterogeneous environments (Andrewartha & Birch
15 1954; Day & Possingham 1995; Hanski 1998). Increasing rates of local extinction are
16 symptomatic of regional population declines and the fraction of habitat patches that are occupied
17 is often related to metapopulation persistence (Lande 1987; Vos *et al.* 2001; but see Elkin &
18 Possingham 2008). Dispersal is important for the recolonisation of vacant habitat patches,
19 regulation of local population dynamics and reducing extinction risk in spatially structured
20 populations (Bowler & Benton 2005).

21 Dispersal between populations in heterogeneous landscapes is one of the most important,
22 yet least understood, ecological processes related to the persistence of animal populations
23 (Bowler & Benton 2005). Although often assumed to be symmetric in spatial population

1 models (Kleinhans & Jonsson 2011), dispersal is a complex trait regulated by independent
2 processes operating during emigration, immigration and transition (Bowler & Benton 2005). Not
3 only are there multiple stages of dispersal, but the same proximate factor may have
4 compensatory effects on the different stages of dispersal (Ims & Hjermann 2001). For example,
5 high local population density often promotes emigration, but tends to inhibit immigration (Ims &
6 Hjermann 2001). This imbalance between the emigration and immigration stages of dispersal is
7 an important cause of asymmetry in dispersal rates (Kawecki & Holt 2002). There is
8 accumulating evidence that asymmetric dispersal is the rule rather than the exception in a wide
9 range of animal taxa (Senar, Conroy & Borrás 2002; McIntire, Schultz & Crone 2007; Smith *et*
10 *al.* 2008).

11 The identification of populations functioning as net exporters of dispersing individuals,
12 due to asymmetric dispersal, is becoming increasingly important to biological conservation
13 (Donovan *et al.* 1995). Asymmetric dispersal of individuals into populations that are likely to go
14 locally extinct (Vuilleumier & Possingham 2006; Elkin & Possingham 2008) and net movement
15 into recently modified landscapes (Remeš 2000; Battin 2004) are detrimental to long-term
16 metapopulation persistence. However, asymmetric dispersal from source to sink populations
17 may stabilize asynchronous population dynamics in modified landscapes (Doebeli 1995), prevent
18 population declines (With, Schrott & King 2006) and allow populations to persist in landscapes
19 degraded by habitat loss (Brown & Kodric-Brown 1977; McIntire, Schultz & Crone 2007). The
20 effects of landscape change on the three stages of dispersal (emigration, immigration and
21 transition) often have multiple consequences for animal populations (Bowler & Benton 2005).
22 For example, habitat loss may limit emigration through within-population processes such as
23 increased reproduction and depressed survival (Pulliam & Danielson 1991), but habitat loss may

1 also inhibit transition rates through between-population processes such as increased dispersal
2 mortality and reduced landscape permeability (Gustafson & Gardner 1996). Effective landscape
3 conservation thus requires understanding of asymmetric dispersal in terms of within-population
4 processes, such as emigration and immigration, as well as between-population processes, such as
5 inter-patch movement and landscape connectivity (Haynes *et al.* 2007; Revilla & Wiegand
6 2008). In addition, knowledge about the mechanisms of landscape change (Fahrig 2003; Fischer
7 & Lindenmayer 2007) and the relative influence of habitat loss and habitat fragmentation on
8 asymmetric dispersal are necessary for landscape management for wildlife conservation
9 (Wiegand, Revilla & Moloney 2005; With, Schrott & King 2006).

10 Recently developed population genetic models allow the estimation of bidirectional
11 migration rates over ecologically relevant time frames and can approximate biologically realistic
12 scenarios such as asymmetric dispersal (Pearse & Crandall 2004). One such model uses
13 coalescent theory (Kingman 1982) to approximate the genealogical history of genetic samples
14 backward in time to estimate the number of immigrants per generation that originated in other
15 sampled populations (Beerli & Felsenstein 2001; Wakeley 2001). This analytic approach has
16 proved useful for identifying the dynamics of asymmetric dispersal and effective population
17 sizes expected under source-sink population structure (Fraser *et al.* 2007).

18 In this paper, field survey and molecular data were used to evaluate *a priori* hypotheses
19 for the effects of landscape change on patch occupancy and asymmetric migration in a spatially
20 structured rainforest bird population. We estimated logrunner (*Orthonyx temminckii*, Ranzani
21 1822) occupancy rates for 46 rainforest patches in a regional study area and quantified
22 bidirectional genetic migration rates among 11 logrunner populations in a portion of the study
23 area. Our research objectives were to 1) investigate spatial variation in logrunner patch

1 occupancy rates to determine the relative effects of landscape composition, landscape change
2 and patch structure on local extinction, 2) determine the extent to which emigration and
3 immigration rates were asymmetric, 3) evaluate spatial variation in emigration and immigration
4 rates to discover the relative influence of local and between-population landscapes on
5 asymmetric dispersal, and 4) investigate spatial variation in emigration and immigration rates to
6 determine the relative contributions of habitat loss and habitat fragmentation to asymmetric
7 dispersal.

8

9 **Materials and methods**

10 **STUDY SPECIES**

11 We selected the logrunner to investigate the effects of landscape change on patch
12 occupancy and asymmetric dispersal because specialised life-history traits may predispose this
13 species to local extinction and restricted dispersal (Sodhi, Liow & Bazzaz 2004; Fahrig 2007).
14 Logrunners are ground-dwelling Passerines (Family Orthonychidae) endemic to subtropical
15 rainforests of south-eastern Australia (Higgins & Peter 2002). The adults are sedentary, maintain
16 year-round home ranges and natal dispersal is the primary mode of dispersal between
17 populations. Because logrunners possess short rounded wings and a partially atrophied sternum,
18 they have a limited ability for sustained flight. In addition, this species has highly specialised
19 morphological and behavioural adaptations for terrestrial foraging in the leaf litter of rainforests
20 (Higgins & Peter 2002).

21 Previous research indicated the connectivity of logrunner populations was historically
22 limited by the extent of dry eucalypt (*Eucalyptus* spp.) forest, but naturally heterogeneous
23 landscapes with inter-dispersed patches of rainforest facilitated gene flow (Pavlacky *et al.* 2009).

1 In addition, there was evidence for a contemporary shift in the pattern of dispersal, with
2 deforestation having become the most important barrier to migration between logrunner
3 populations. The generation time of logrunners was estimated to be four years, which suggested
4 approximately 25 generations have elapsed since deforestation began in the early 1900s
5 (Pavlacky *et al.* 2009).

6

7 STUDY AREA

8 The regional study area for the investigation of logrunner site occupancy (8,049 km²) was
9 located within the South East Queensland Biogeographic Region, Australia (27°30'-28°23'S,
10 152°30'-153°38'E) (Fig. 1). This area included several World Heritage sites that are part of the
11 Gondwana Rainforests of Australia, including Lamington, Moogerah Peaks, Mount Barney,
12 Mount Chinghee, Tamborine and Springbrook National Parks, as well as rainforest remnants on
13 private land. Eucalypt forest was the dominant vegetation type with rainforest on the mountain
14 tops, and in alluvial fans and wet gullies. A reconstruction of historic forest structure (EPA
15 2004) within the regional study area showed rainforest cover had decreased by 52% since the
16 early 1900s and occupied 4% of the land area at the time of this study (Pavlacky 2008).

17 The study area for the genetic analyses of dispersal covered a portion (415 km²) of the
18 regional study area (28°07'19"- 28°16'37"S, 153°05'59"-153°19'49"E) on the McPherson
19 Range, including Lamington and Springbrook National Parks, and private land holdings (Fig. 1).
20 The contemporary landscape was composed of 38% subtropical rainforest, 36% eucalypt forest,
21 21% deforested land and 4% second-growth forest (Pavlacky *et al.* 2009). A reconstruction of
22 the historic landscape structure (EPA 2004) in the dispersal study area indicated 27% of the
23 rainforest cover had been lost to deforestation over the previous 100 years (Pavlacky 2008).

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OCCUPANCY SAMPLING

We used a two-way random stratified sample design to select 46 rainforest patches from the regional study area (Pavlacky 2008). We stratified the patches into three rainforest types: 1) upland notophyll vine forest; 2) lowland notophyll vine forest; and 3) Araucarian (*Araucaria cunninghamii*) notophyll-microphyll vine forest (Webb, Tracey & Williams 1984). Upland rainforests occurred between 800-900 m, lowland forests below 700 m and Araucarian rainforests below 700 m on dry, well drained slopes and foothills (Webb, Tracey & Williams 1984). For each rainforest type, we randomly selected nine small (2.5 - 16.7 ha), three intermediate (20.2 - 75.9 ha) and three large (> 189.0 ha) rainforest patches. We sampled one additional intermediate-sized patch for Araucarian rainforest. For the purpose of this study, we combined lowland and Araucarian rainforest occurring below 700 m to represent lowland rainforests.

D. Pavlacky surveyed logrunners by sight and song along a single transect within each of the 46 rainforest patches from 02 November 2004 - 21 January 2005 and 29 October 2005 - 08 January 2006. The surveys occurred shortly after the logrunner breeding season (April - October) during the fledgling to independence period (Higgins & Peter 2002). Along each transect, we sampled logrunners at 4 - 8 unlimited-distance point count stations between 0.5 and 4 hrs after sunrise, for durations of 10 min at each station. We located the point counts at 100-m intervals along the line transects using a systematic design with a random start. The mean transect length was 605 m and the mean number of points per transect was 6.7, which, based on the estimated population density and effective detection radius (not shown), intersected approximately three logrunner territories. We recorded point-specific covariates for time of day,

1 as well as survey-specific covariates for year and time of year to account for potential
2 heterogeneity in logrunner detection probabilities (Pavlacky 2008).

3

4 GENETIC SAMPLING

5 Between 2001 and 2006, we captured and sampled 220 logrunners at 11 rainforest sites
6 using a systematic sampling design, with nine eastern locations separated by ~5 km and two
7 western sites separated by ~10 km (Pavlacky *et al.* 2009). We selected the sample locations to
8 ensure the local and between-population landscapes varied in the composition and configuration
9 of forest types, as well as to ensure the landscapes varied in the degree of habitat loss and
10 fragmentation (Fig. 1). We lured birds into a 9 m-long, 2.5 m-high, 38 mm-mesh mist-net using
11 broadcasts of territorial vocalizations from two 4W speakers arranged on either side of the net
12 lane. For each bird captured, we obtained a 40 - 60 μ l blood sample from the brachial vein. The
13 samples were stored in Queens' lysis buffer solution.

14 We extracted DNA from the blood samples using an ammonium acetate salting-out
15 method and amplified 10 microsatellite markers using the Polymerase Chain Reaction (PCR)
16 protocol of Nicholls *et al.* (2007). The primers were fluorescently labelled and the PCR products
17 were sized using capillary electrophoresis (MegaBACE 500, Amersham Biosciences). The mean
18 genotyping error per locus over the 10 loci for this study was 0.0063 (Pavlacky *et al.* 2009). We
19 evaluated the performance of the 10 microsatellite loci; two loci exhibited high frequencies of
20 null alleles, and therefore we used eight loci for the final analyses. In addition, we evaluated
21 Hardy-Weinberg and migration-drift equilibrium assumptions, which were necessary for the
22 population genetic analysis of allele frequency data (Beerli & Felsenstein 1999; Pearse &
23 Crandall 2004). All populations except one (Sarabah) were within Hardy-Weinberg equilibrium.

1 A coalescent-based, Markov chain Monte Carlo simulation indicated the logrunner populations
2 were at migration-drift equilibrium. The logrunner populations demonstrated low but
3 statistically significant genetic differentiation ($F_{ST} = 0.015$; SE = 0.005; 95% CI = 0.005, 0.025),
4 and 33 of the 55 pair-wise estimates of F_{ST} were statistically different (Pavlacky *et al.* 2009).

5

6 LANDSCAPE STRUCTURE

7 The landscape structure immediately surrounding the sampled population represented
8 local landscapes and the landscapes separating the sampled populations represented the between-
9 population landscapes. Little was known about the home range size and dispersal ecology of
10 logrunners, but specialised life history traits suggested this species was sedentary with limited
11 dispersal ability (Higgins & Peter 2002). We chose a 2-km radius to characterise local
12 landscapes on the basis that more woodland bird species with limited dispersal ability responded
13 to landscape features within 2 km than at larger scales (Westphal *et al.* 2003). We characterised
14 the structure of the local landscape surrounding each sample location using the pre-clearing and
15 current data on vegetation types (regional ecosystems; EPA 2004) and ArcGIS version 9.1 (ESRI
16 2005). At each sample location, we centred a 2 km-radius circular buffer on the mean UTM
17 coordinates of the point count and capture locations (Pavlacky 2008). We clipped the land-cover
18 from the pre-clearing and current regional ecosystem data layers using the circular buffer.
19 Within each of the historic and contemporary 12.6 km² landscapes, we recorded the forest type
20 of the sampled locations, and measured the total area of rainforest cover (km²) and the mean area
21 of rainforest patches (km²) using ArcGIS. We estimated percentage of rainforest cleared and the
22 reduction in mean patch size by calculating the percent change between the pre-clearing and
23 current landcover data (Table 1). We measured mean patch isolation in the regional study area

1 as the mean distance (km) from the sampled patch to the edge of the nearest patch (> 2.5 ha) in
2 each of four quadrants delineated by the cardinal directions (Table 1).

3 For the between-population landscapes, we used 0.5 km-wide landscapes between
4 logrunner populations to represent the vegetation encountered by dispersing individuals and to
5 represent multiple dispersal pathways. The 0.5 km-wide buffer distance was approximately five
6 times as wide as a typical logrunner territory. This buffer width minimised the area of overlap
7 between adjacent landscapes and maximised the coverage of the dispersal study area. The 0.5
8 km-wide landscapes effectively described the negative effect of deforestation and patch
9 configuration on symmetric migration between logrunner populations (Pavlacky *et al.* 2009).
10 We characterised the structure of between-population landscapes intervening the sample
11 locations using the contemporary regional ecosystem data (EPA 2004) and ArcGIS version 9.1
12 (ESRI 2005). We constructed 0.5 km-wide buffers centred on straight-line vectors between each
13 pair of sample locations, and clipped the land-cover from the contemporary regional ecosystem
14 data layer to the extent of the buffers (Pavlacky *et al.* 2009). Within each 0.5 km-wide buffer,
15 we measured the percent cover of rainforest, wet eucalypt forest, deforested land and forest patch
16 density (Table 1). We calculated the density of all distinct forest patches in the buffers as the
17 number of patches per km². The mean area of the buffers used to estimate the structure of the
18 between-population landscapes was 4.9 km² (SD = 2.1). The total area sampled in the 55
19 landscape buffers was 269 km², which resulted in a comprehensive coverage of the 240 km²
20 study area with minimal overlap among the buffers.

21

22 OCCUPANCY ESTIMATION

23 We estimated logrunner detection (p) and occupancy (ψ) probabilities using a zero-

1 inflated binomial model (MacKenzie *et al.* 2002; Tyre *et al.* 2003) implemented in the software
2 programs MARK (White & Burnham 1999) and PRESENCE (Hines 2006). We used MARK for
3 model construction, estimation and selection, and PRESENCE for assessing model fit. We
4 estimated detection probabilities from spatially replicated point count surveys within a single
5 visit (MacKenzie *et al.* 2006). The model estimated the probability (p_{it}) that the species was
6 detected at replicated point count survey t , given presence at site i , and the probability (ψ_i) that
7 the species was present at site i (MacKenzie *et al.* 2002). We modelled the detection (p_{it}) and
8 occupancy (ψ_i) parameters as functions of survey and/or site-specific covariates using the logit
9 link function (MacKenzie *et al.* 2002). Categorical covariates were coded as indicator variables
10 and continuous covariates were standardised using the z -transformation. We constructed the
11 occupancy models using all subsets of the three detection covariates (rainforest type, time of day
12 and ordinal date) and six occupancy covariates (Table 1) with an upper limit of five covariates,
13 which resulted in a candidate set of 130 models. We evaluated the goodness-of-fit for the global
14 model (number of parameters $K = 9$) using the Pearson statistic and 10,000 parametric
15 bootstrap iterations in program PRESENCE (MacKenzie & Bailey 2004).

16

17 MIGRATION ESTIMATION

18 We used genetic estimates of migration within the expected dispersal distance of the
19 species to infer dispersal success (Rousset 2001), which was defined as dispersal from a natal
20 area to an area where breeding first takes place (Greenwood & Harvey 1982). We used the
21 structured coalescent model in program MIGRATE version 2.1.3 to estimate the migration rate
22 per generation $M_{ji} = m_{ji} / \mu$ and effective population size $\theta_i = 4N_e\mu$, where m_{ji} was the number of
23 immigrants per generation from subpopulation j into subpopulation i , N_e was the effective

1 population size for subpopulation i , and μ was the locus specific mutation rate per generation
2 (Beerli & Felsenstein 2001). We held the mutation rate μ constant across all eight loci and
3 modelled μ according to the step-wise mutation model (Pavlacky 2008). The migration rates M_{ji}
4 between all 110 population pairs were estimated within an unconstrained migration matrix. The
5 unconstrained parameterisation allowed the effective population size θ_i to vary by subpopulation
6 and thus did not assume equal population sizes. We calculated the starting parameter values
7 from the mean parameter estimates over four preliminary analyses. We ran the model with a
8 burn-in of 10,000 iterations, 10 short chains (1,000 sampled genealogies), two long chains
9 (10,000 sampled genealogies) and sampled one of every 20 constructed genealogies. We used
10 the moving steps option to ensure a minimum tree acceptance of 200 genealogies for short chains
11 and 2,000 genealogies for long chains. We accounted for variation between independent model
12 runs by estimating the final parameters over 10 replicates of the model (Pavlacky 2008).

13 The assumptions of the structured coalescent model were 1) Wright-Fisher random
14 mating within populations, 2) migration-drift equilibrium and 3) constant effective population
15 sizes and mutation rates through time (Beerli & Felsenstein 1999). Assumption 1) was satisfied
16 for all populations except Sarabah (see Genetic Sampling section). Assumption 2) was verified
17 using a coalescent simulation, which indicated sufficient time since habitat loss has elapsed for
18 the pattern of migration and genetic drift to stabilise (Pavlacky *et al.* 2009). Assumption 3),
19 constant effective population sizes over time, may be questionable in local landscapes
20 experiencing as much as 54% habitat loss (Table 1). However, the estimates of migration and
21 effective population size are long-term averages heavily weighted by coalescent events the recent
22 past (Beerli 2009). Because assumption 2) indicated sufficient time has elapsed for the pattern of
23 migration to stabilise, the estimates of migration and effective population size likely reflect

1 contemporary landscape conditions rather than non-equilibrium reductions in population size
2 from past habitat loss. In addition, high levels of immigration are capable of arresting population
3 declines in landscapes impacted by habitat loss (With, Schrott & King 2006). The lack of a
4 correlation between effective population size and habitat loss (see below) provided little
5 evidence for a relationship between current effective population size and past habitat loss.

6 We grouped the migration rates according to their respective emigration and immigration
7 populations and stacked the data to represent 110 emigration and 110 immigration rates ($n =$
8 220). A generalized linear model with the normal distribution and identity link function (Nelder
9 & Wedderburn 1972; PROC GENMOD, SAS Institute 2008) was used to investigate the
10 asymmetry of logrunner migration rates. We used an analysis of variance parameterization and
11 likelihood ratio test to investigate the difference between the emigration and immigration rates
12 nested within the 11 populations. The 95% confidence intervals for the parameter estimates
13 were calculated using likelihood profiles. We evaluated the fit of the migration data to a normal
14 distribution using the Kolmogorov-Smirnov goodness-of-fit test (PROC UNIVARIATE, SAS
15 Institute 2008).

16 We modelled the logrunner emigration ($n = 110$) and immigration ($n = 110$) rates as a
17 function of local and between-population landscape features using a generalized linear mixed
18 model with the normal distribution and identity link function (PROC GLIMMIX, SAS Institute
19 2008; Bolker *et al.* 2009). The emigration and immigration models included block covariance
20 structures for the respective emigration and immigration populations, and population pairs. This
21 within- and between-covariance structure permitted landscape covariates on directional
22 migration within populations and directional migration between populations, and appropriately
23 accounted for the non-independence of the clustered observations. We evaluated all subsets of

1 the covariance structures for the full fixed-effect models (number of parameters $K = 8$) using
2 restricted maximum pseudo-likelihood (RSPL) and likelihood ratio tests. After selecting an
3 appropriate error structure for the models, we estimated the model parameters using the Laplace
4 maximum likelihood approximation. The best covariance structure for the emigration data
5 included random effects for the 11 emigration populations and 55 population pairs ($\sigma^2 = 6.0$; $P =$
6 0.020). The best covariance structure for the immigration data included random effects for the
7 11 immigration populations and 55 population pairs ($\sigma^2 = 11.7$; $P = 0.001$). After determining
8 the appropriate covariance structure for the data, we ran all one and two variable subsets of the
9 fixed effect covariates in Table 1, which resulted in candidate sets of 45 models for emigration
10 and immigration. We calculated 95% confidence intervals for the fixed-effect parameters using
11 the t distribution and the covariance parameters using likelihood profiles. We investigated co-
12 linearity among the predictor variables (Table 1) using the Spearman rank-order correlation
13 (PROC CORR, SAS Institute 2008), and all pairs of variables exhibited correlations $|r| < 0.7$,
14 with exception of rainforest lost and patch area lost ($r = 0.75$). In addition, correlations between
15 logrunner effective population size (θ_i) and the amount of rainforest lost and mean patch area lost
16 in local landscapes were investigated using the Spearman rank-order correlation ($n = 11$), and no
17 relationship between θ_i and the landscape modification variables was found ($r > -0.08$, $P > 0.81$).

18

19 HYPOTHESES AND MODEL JUSTIFICATION

20 We used predictive models and the method of multiple working hypotheses (Chamberlain
21 1965) to evaluate *a priori* hypotheses for how landscape processes could influence the patch
22 occupancy and between-population migration rates of logrunners. Objective 1) investigated
23 spatial variation in logrunner patch occupancy rates to determine the relative influence of

1 landscape and patch structure on local extinction. We hypothesised that patch occupancy was a
2 function of 1.1) landscape composition, 1.2) habitat loss and habitat fragmentation, and 1.3) the
3 area and isolation of rainforest patches. We also evaluated three hypotheses for logrunner
4 detection probabilities, which proposed that detection varied by rainforest type, time of year,
5 time of day. We assumed that declining occupancy rates in response to landscape modification
6 over time would be indicative of local extinction, while declining occupancy in response to
7 increasing patch isolation would be symptomatic of restricted dispersal and reduced colonisation
8 of isolated patches (Hanski 1998). We adopted a species-oriented approach for representing
9 landscape change (Fischer & Lindenmayer 2007), where habitat loss was represented by
10 percentage of rainforest lost and habitat fragmentation was represented by the percent change of
11 mean rainforest patch size over time. Hypothesis 1.1) was represented by models containing the
12 rainforest cover and forest type variables, hypothesis 1.2) by models containing the rainforest
13 cover lost and patch area lost variables, and hypothesis 1.3) by the patch area and isolation
14 variables (Table 1).

15 To address objective 2), we investigated emigration and immigration rates to determine
16 the degree of asymmetric dispersal between logrunner populations. Hypothesis 2.1) proposed
17 that dispersal rates were symmetric and hypothesis 2.2) proposed that dispersal rates were
18 asymmetric. Evidence for asymmetric dispersal was inferred when populations demonstrated net
19 emigration or net immigration (Kawecki & Holt 2002).

20 After establishing the extent of asymmetric dispersal, objective 3) investigated spatial
21 variation in emigration and immigration rates to determine how local and intervening landscapes
22 influenced asymmetric dispersal between logrunner populations. We hypothesised that
23 emigration and immigration were related to 3.1) the composition and modification of local

1 landscapes and 3.2) the composition and configuration of the between-population landscapes.
2 Our inference about the effects of landscape structure on emigration and immigration was based
3 on the perspective that the composition and modification of local landscapes would influence
4 asymmetric dispersal by within-population vital rates (Pulliam 1988; Revilla & Wiegand 2008),
5 whereas the composition and configuration of intervening landscapes would influence
6 asymmetric dispersal through between-population landscape connectivity (Gustafson & Gardner
7 1996; Haynes *et al.* 2007). Hypothesis 3.1) was represented by models containing the forest
8 type, rainforest cover, rainforest cover lost, and patch area lost variables measured in local
9 landscapes, and hypothesis 3.2) by the rainforest cover, wet eucalypt forest cover, deforested
10 land cover, and forest patch density variables measured in the between-population landscapes
11 (Table 1). We also evaluated a null hypothesis that emigration and immigration were related to
12 the distance between the populations.

13 Objective 4) investigated emigration and immigration rates to determine the relative
14 contributions of habitat loss and habitat fragmentation to asymmetric dispersal between
15 logrunner populations. We hypothesised that spatial variation in emigration and immigration
16 rates were a function of 4.1) habitat loss and 4.2) habitat fragmentation in local landscapes.
17 These two hypotheses reflected the perspective that spatial patterns of landscape change can
18 influence the extent of asymmetric dispersal (With, Schrott & King 2006). Because large
19 populations are often characterized by net emigration and small populations by net immigration
20 (Stacey & Taper 1992), we expected that habitat loss and fragmentation would reduce population
21 size (Bender, Contreras & Fahrig 1998) and produce asymmetric migration between the
22 modified and intact landscapes. Hypothesis 4.1) was represented by the loss of rainforest cover
23 over time and hypothesis 4.2) was represented by the reduction in patch size over time (Table 1).

1

2 MODEL SELECTION

3 We estimated the relative Kullback-Leibler Information lost when models are used to
4 approximate reality using the Akaike Information Criterion adjusted for sample size (AIC_c)
5 (Burnham & Anderson 2002). We ranked the models by ΔAIC_c , measured the strength of
6 evidence for alternate hypotheses by AIC_c weights (w_i), and quantified the likelihood of the
7 modelled hypotheses given the data by evidence ratios (w_i / w_j). The relative importance of the
8 hypotheses and predictor variables were quantified by cumulative AIC_c weights [$w_+(j)$]. We
9 calculated model averaged predictions and parameter estimates, and unconditional standard
10 errors and 95% confidence intervals for model sets defined by the 0.135 evidence ratio ($AIC_c <$
11 4). We determined the strength of evidence for effect sizes by evaluating the model averaged
12 parameter estimates () with respect to zero using unconditional standard errors and 95%
13 confidence intervals (Burnham & Anderson 2002).

14

15 **Results**

16 PATCH OCCUPANCY

17 Multi-model inference for the effects of landscape features on logrunner patch occupancy
18 indicated slightly more support for the patch area and isolation hypothesis [$w_+(j) = 0.98$] than the
19 habitat loss and fragmentation hypothesis [$w_+(j) = 0.74$]. The patch area and isolation hypothesis
20 was 17 times more probable, and the habitat loss and fragmentation hypothesis was 12 times
21 more probable than the landscape composition hypothesis [$w_+(j) = 0.06$]. Cumulative AIC_c
22 weights indicated patch isolation [$w_+(j) = 0.96$], habitat loss [$w_+(j) = 0.45$] and habitat
23 fragmentation [$w_+(j) = 0.28$] were the best predictors of logrunner patch occupancy. Rainforest

1 forest type, remnant rainforest cover and patch area demonstrated much lower ability to predict
 2 logrunner occupancy [$w_+(j) < 0.04$]. The habitat loss hypothesis was twice as probable as the
 3 habitat fragmentation hypothesis. Logrunner detection probabilities were best predicted by
 4 rainforest type [$w_+(j) = 0.91$], followed by time of day [$w_+(j) = 0.25$] and time of year [$w_+(j) =$
 5 0.04].

6 Logrunner patch occupancy was best predicted by a model containing mean patch
 7 isolation and habitat loss (Table 2). Occupancy declined with increasing mean patch isolation
 8 ($\beta_{Patch\ isolation} = -2.83$; SE = 1.19; CI = -5.16, -0.49) and the percentage of rainforest cover lost
 9 since settlement (Table 3; Fig. 2), and the 95% confidence intervals for these effects excluded
 10 zero (Table 3). There was nearly equal support for the second best model containing the effects
 11 of mean patch isolation and patch area lost (Table 2). Logrunner occupancy declined with
 12 increasing patch isolation and patch area lost ($\beta_{Patch\ area\ lost} = -2.56$; SE = 1.36; CI = -5.23, 0.11)
 13 (Fig. 2). The 95% confidence interval for the effect of patch area lost narrowly covered zero,
 14 indicating a marginal effect size. There was also support for the third best model containing only
 15 the effect of mean patch isolation, but this model was two times less probable than the best
 16 approximating model (Table 2). The goodness-of-fit test indicated the full model fit the data
 17 reasonably well ($\chi^2 = 537.0$; $P = 0.199$).

18

19 ASYMMETRIC MIGRATION

20 The emigration and immigration rates for the 11 logrunner populations were asymmetric
 21 ($\chi^2 = 37.5$; $P < 0.001$). The 95% confidence intervals of the effects with respect to zero
 22 indicated emigration exceeded immigration for the Binna Burra ($\beta_{Binna\ Burra} = 4.9$; SE = 1.2; CI =
 23 1.5, 8.3) and Sarabah ($\beta_{Sarabah} = 5.5$; SE = 1.2; CI = 2.1, 8.9) populations, while emigration was

1 less than immigration for the Fairview ($\beta_{Fairview} = -4.0$; SE = 1.2; CI = -7.4, -0.6), Numinbah
 2 ($\beta_{Numinbah} = -3.8$; SE = 1.2; CI = -7.2, -0.4) and Warrie ($\beta_{Warrie} = -5.1$; SE = 1.2; CI = -8.5, -1.7)
 3 populations. The migration data fit the normal distribution ($D = 0.07$; $P > 0.150$).

4

5 DO LOCAL OR BETWEEN-POPULATION LANDSCAPES INFLUENCE EMIGRATION 6 AND IMMIGRATION?

7 Multi-model inference for emigration into logrunner populations indicated the local
 8 landscape hypothesis [$w_+(j) = 0.97$] was three times more probable than the between-population
 9 landscape hypothesis [$w_+(j) = 0.33$]. Cumulative AIC_c weights indicated mean patch area lost in
 10 local landscapes [$w_+(j) = 0.71$] was the best predictor of logrunner emigration, followed by forest
 11 type [$w_+(j) = 0.23$], rainforest cover [$w_+(j) = 0.21$] and rainforest lost [$w_+(j) = 0.20$] in local
 12 landscapes. The effect of patch area lost on emigration was seven times more probable than the
 13 effect of distance between the populations [$w_+(j) = 0.10$], and rainforest cover and rainforest lost
 14 were two times more probable than distance. The between-population landscape variables, patch
 15 density, deforested land, rainforest cover and wet eucalypt cover, exhibited much low predictive
 16 ability [$w_+(j) < 0.12$].

17 Emigration into logrunner populations was best predicted by mean patch area lost and the
 18 amount of remnant rainforest cover in local landscapes (Table 2). Emigration declined with
 19 increasing mean patch area lost ($\beta_{Patch\ area\ lost} = -0.048$; SE = 0.017; CI = -0.083, -0.014) and
 20 increased with increasing remnant rainforest cover in local landscapes (Table 3; Fig. 3). The
 21 95% confidence interval for the effect of mean patch area lost did not cover zero and the interval
 22 for the effect of remnant rainforest cover narrowly covered zero (Table 3), indicating large and
 23 marginal effect sizes, respectively. There was nearly equal support for the second best model

1 containing only the effect of mean patch area lost (Table 2). The addition of the other predictor
 2 variables did not appreciably increase model fit as measured by the log likelihood (Table 2), and
 3 the 95% confidence intervals for these effects substantially covered zero. For example, there
 4 was little evidence for an effect of distance on emigration in the fifth best model ($\beta_{Distance} = -0.09$;
 5 $SE = 0.11$; $CI = -0.31, 0.13$).

6 Multi-model inference for immigration from logrunner populations showed equal support
 7 for the local landscape [$w_+(j) = 0.82$] and between-population landscape [$w_+(j) = 0.80$]
 8 hypotheses. Cumulative AIC_c weights [$w_+(j)$] indicated mean patch area lost in local landscapes
 9 [$w_+(j) = 0.51$] and forest patch density in the between-population landscapes [$w_+(j) = 0.46$] were
 10 the best predictors of logrunner immigration, followed by rainforest lost in local landscapes
 11 [$w_+(j) = 0.21$] and rainforest cover in between-population landscapes [$w_+(j) = 0.17$]. The effects
 12 of local patch area lost and intervening forest patch density on immigration were six times more
 13 probable than the effect of distance between the populations [$w_+(j) = 0.08$]. Wet eucalypt forest
 14 and deforested cover in the between-population landscapes, and forest type and rainforest cover
 15 in local landscapes exhibited low predictive ability [$w_+(j) < 0.13$].

16 Immigration from logrunner populations was best predicted by mean patch area lost in
 17 local landscapes and forest patch density in between-population landscapes (Table 2).
 18 Immigration increased with increasing mean patch area lost in local landscapes ($\beta_{Patch\ area\ lost} =$
 19 0.052 ; $SE = 0.020$; $CI = 0.012, 0.093$) and declined with increasing forest patch density in the
 20 between-population landscapes ($\beta_{Forest\ patch\ density} = -0.349$; $SE = 0.148$; $CI = -0.640, -0.059$)
 21 (Table 3; Fig. 3). The 95% confidence intervals for the effects of reduced mean patch size and
 22 forest patch density did not cover zero, indicating large effect sizes for these variables. As with
 23 emigration, there was little evidence for an effect of distance on immigration.

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DOES HABITAT LOSS OR FRAGMENTATION INFLUENCE EMIGRATION AND IMMIGRATION?

Multi-model inference for emigration into logrunner populations indicated the habitat fragmentation hypothesis [$w_+(j) = 0.71$] was four times more probable than the habitat loss hypothesis [$w_+(j) = 0.20$]. As presented in the previous section, logrunner emigration was best predicted by a model containing the negative effect of mean patch area lost (Tables 2 and 3; Fig. 3). There was support ($AIC_c < 4$) for models containing the negative effects of rainforest cover lost ($Rainforest\ lost = -0.058$; $SE = 0.032$; $CI = -0.122, 0.006$), but these models were five times less probable than the best approximating model containing the fragmentation effect (Table 2).

Multi-model inference for immigration from logrunner populations indicated the habitat fragmentation hypothesis [$w_+(j) = 0.51$] was two times more probable than the habitat loss hypothesis [$w_+(j) = 0.21$]. As presented above, logrunner immigration was best predicted by a model containing the positive effect of mean patch area lost (Tables 2 and 3; Fig. 3). There was support ($AIC_c < 4$) for the second best model containing the positive effect of rainforest cover lost ($Rainforest\ lost = 0.071$; $SE = 0.033$; $CI = 0.005, 0.138$), but this model was three times less probable than the best approximating model containing the fragmentation effect (Table 2).

Discussion

The occurrence of logrunner populations in our study region was primarily influenced by rainforest patch structure and anthropogenic landscape change. Patch isolation was the best predictor of logrunner patch occupancy, with smaller effects of rainforest loss and fragmentation over time. Patch area, remnant rainforest cover and rainforest type had very little influence on

1 logrunner occupancy rates. The large effect of patch isolation suggested dispersal and
2 colonization from neighbouring habitat patches were important processes for maintaining
3 regional patch occupancy (Hanski 1998). However, after controlling for patch isolation, the loss
4 and fragmentation of rainforest over time influenced patch occupancy rates to a greater extent
5 than patch isolation alone. This suggested that immigration from adjacent patches was unable to
6 prevent local extinction in landscapes that have experienced high levels of habitat loss and
7 fragmentation. Moreover, the occurrence of logrunner populations was primarily influenced by
8 habitat loss over the past 100 years since European settlement, while reduction of mean patch
9 size over time and associated edge effects were less important. This result provided little support
10 for the hypothesis that habitat fragmentation was more important than habitat loss for explaining
11 local extinction of a highly specialised rainforest species (Bender, Contreras & Fahrig 1998;
12 Fahrig 2003).

13 The patch occupancy study indicated that dispersal from surrounding rainforest patches
14 and anthropogenic landscape change played important roles for the occurrence of logrunner
15 populations. We investigated spatial variation in emigration and immigration rates to gain a
16 mechanistic understanding of how landscape composition and modification influences dispersal
17 between logrunner populations. Our results suggested the effects of landscape change on
18 asymmetric dispersal played an important role in local extinction of logrunner populations.
19 However, the differences in the landscape structure of the regional and dispersal study areas may
20 have limited our ability to make inferences about the relationship between asymmetric dispersal
21 and local extinction. The occupancy study occurred in a large region with 4% rainforest cover
22 and 52% habitat loss, and dispersal study occurred in a portion of the region with 38% rainforest
23 cover and 21% habitat loss (Fig. 1). The local landscapes for the occupancy study contained on

1 average 27% rainforest cover and 37% habitat loss, whereas the landscapes for the dispersal
2 study contained on average 42% rainforest cover and 25% habitat loss (Table 1). The large
3 degree of asymmetric dispersal at moderate levels of landscape modification suggested the
4 effects of landscape change on dispersal between logrunner populations may be larger in the
5 regional study area than reported for the dispersal study area. Nevertheless, the regional
6 occupancy study controlled for variation in patch isolation, making the landscape effects
7 comparable in the regional and dispersal study areas. Finally, although the sizes of the local and
8 between-population landscapes were based on logrunner life history, the scale of the landscape
9 measurements may have interfered with our ability to evaluate the relative effects of habitat loss
10 and fragmentation on occupancy and asymmetric dispersal (Smith, Fahrig & Francis 2011).

11 The comparison of emigration and immigration rates indicated a high degree of
12 asymmetric dispersal between the 11 populations. The migration rates reported in this study can
13 be considered effective dispersal, or natal dispersal to an area where successful breeding
14 occurred. The estimates of effective dispersal reflected long-term averages of the number
15 migrants per generation, and thus were useful for approximating the dispersal dynamics of
16 logrunners since European landscape change began in the early 1900's. The Binna Burra and
17 Sarabah populations in contiguous upland and lowland forests of Lamington National Park (427
18 km²) were net exporters of dispersing logrunners, while the Fairview and Warrie populations in
19 contiguous lowland forests of Springbrook National Park (37 km²), as well as the Numinbah
20 population in a small isolated lowland patch (1 km²) were net importers of dispersing birds.
21 Relatively intact landscapes were net exporters and landscapes experiencing large reductions in
22 mean rainforest patch size over time were net importers of dispersing logrunners. In fact, a
23 greater than 60% reduction in mean patch size over time was capable of switching populations

1 from net exporters to net importers of dispersing logrunners. For example, estimated emigration
2 was 39% greater than immigration in landscapes with an 11% reduction in mean patch size,
3 whereas estimated immigration was 37% greater than emigration in landscapes with a 95%
4 reduction in mean patch size (Fig. 3). The effect of between-population forest patch density on
5 immigration also influenced the extent of asymmetric migration (Fig. 3).

6 The capacity of logrunner populations to produce emigrants that went on to reproduce in
7 other populations was primarily related to the composition and modification of local landscapes.
8 The structure of the intervening landscapes had very little influence on emigration. This
9 indicated that processes occurring within local landscapes were more important than the
10 connectivity of between-population landscapes for maintaining emigration, and suggested that
11 emigration was limited by low reproduction and high mortality in modified local landscapes
12 (Revilla & Wiegand 2008). Local landscape structure was expected to cause variation in
13 population vital rates (Pulliam 1988; Revilla & Wiegand 2008), population size (Stacey & Taper
14 1992), which would have important implications for the generation of surplus individuals that are
15 available to emigrate. On the other hand, between-population processes, such as landscape
16 permeability, boundary effects and mortality during transition (Bowler & Benton 2005),
17 appeared less important for successful emigration. This result contrasts with the findings of
18 Haynes *et al.* (2007) who found the composition of intervening landscapes was more important
19 than local habitat quality for emigration in an experimental invertebrate system.

20 The capacity of logrunner populations to accept immigrants that originated in other
21 landscapes was influenced by the structure of both local and between-population landscapes.
22 Local and intervening landscapes were equally important for successful immigration, suggesting
23 that immigration was influenced by high mortality in modified landscapes, as well as by

1 dispersal mortality and/or landscape connectivity between populations (Revilla & Wiegand
2 2008). We found that intervening landscapes composed of small numbers of large forest patches
3 facilitated logrunner immigration, while landscapes with large numbers of small forest patches
4 inhibited immigration. Our results are similar to those of Revilla and Wiegand (2008) who
5 found that adding dispersal habitat and augmenting patch sizes removed the asymmetry in
6 dispersal and decreased the variability of immigration into source populations.

7 The fragmentation of intervening landscapes can produce patterns of asymmetric
8 dispersal by funnelling potential immigrants away from habitat patches, preventing emigration
9 due to hard edge boundaries or by increasing dispersal mortality (Gustafson & Gardner 1996;
10 Revilla & Wiegand 2008). We used a mixed model approach to account for the non-
11 independence and multiple-membership of the emigration and immigration rates, and this
12 approach was useful for evaluating the relative importance of the between-population landscapes
13 while controlling for the effects of local landscapes. Although between-population landscapes
14 were important for successful immigration, the structure of intervening landscapes was less
15 important for effective emigration. The negative effect of landscape heterogeneity on
16 immigration was sufficient to explain asymmetric dispersal between logrunner populations.
17 These findings suggested that dispersal mortality and/or boundary effects while animals are
18 actively moving between habitat patches (transition stage of dispersal) may be particularly
19 important for successful immigration. Conversely, we found little evidence for dispersal
20 mortality or reluctance to emigrate in response to landscape condition as logrunners dispersed
21 from natal to breeding populations. A previous study demonstrated that symmetric migration
22 between logrunner populations was influenced by the deforestation and heterogeneity of
23 intervening landscapes (Pavlacky *et al.* 2009). The current study evaluated the relative

1 importance of local and between-population landscapes and found that reduced connectivity in
2 the landscape was determined by rainforest fragmentation and a complex pattern of asymmetric
3 dispersal.

4 Similar to the findings of With and King (2001), we found that habitat fragmentation was
5 more important than habitat loss for promoting asymmetric dispersal between logrunner
6 populations. This result supported the hypothesis that species from tropical or subtropical
7 systems are particularly vulnerable to habitat fragmentation (Fahrig 2003; Sodhi, Liow & Bazzaz
8 2004). While habitat loss appeared to be more important for explaining local extinctions in the
9 regional logrunner population, habitat fragmentation had more impact on the direction and extent
10 of dispersal between logrunner populations. Large population sizes and high reproductive rates
11 within intact landscapes were expected to promote emigration, while reduced population sizes
12 and survival in modified landscapes were expected to facilitate immigration (Donovan *et al.*
13 1995; Revilla & Wiegand 2008). In addition, high immigration rates into landscapes
14 experiencing population declines may have reduced the availability of high quality nesting
15 territories, and depressed reproduction and survival rates (Lande 1987; Pulliam & Danielson
16 1991; Kawecki & Holt 2002). This may have further reduced the capacity of populations to
17 produce surplus emigrants. Patch area and edge effects (With & King 2001; Laurance *et al.*
18 2002) appeared to play a bigger role than habitat loss in determining which populations were net
19 exporters and net importers of dispersing logrunners. Although we expected substantial
20 population declines in response to habitat loss and fragmentation (Bender, Contreras & Fahrig
21 1998), there was little evidence for relationships between the effective size of logrunner
22 populations and habitat loss or habitat fragmentation. High net immigration in modified
23 landscapes with no apparent decline in effective population sizes suggested a high level of

1 population turnover, and the population declines appeared to be offset by high immigration rates
2 from intact landscapes (With, Schrott & King 2006).

3

4 CONSERVATION IMPLICATIONS

5 Our results supported simulation studies indicating asymmetric dispersal from landscapes
6 functioning as net exporters of dispersing individuals is important for the conservation of forest
7 dwelling bird populations (Donovan *et al.* 1995; Baillie *et al.* 2000; With, Schrott & King 2006).
8 Conservation measures that maintain large patch sizes in the landscape may promote asymmetric
9 dispersal from intact to fragmented landscapes and allow bird populations to persist in
10 landscapes degraded by habitat loss. Habitat fragmentation had a larger influence on the ability
11 of populations to function as net exporters of dispersing birds than net habitat loss, which
12 suggested the negative effects of habitat loss can to some extent be mitigated by conservation
13 measures that maintain large patch sizes in the landscape (Kareiva & Wennergen 1995; With &
14 King 2001). However, immigration may be unable to prevent local extinction in landscapes
15 experiencing high levels of habitat loss. Fragmented sink landscapes may allow populations to
16 persist until habitat restoration can re-establish more extensive forests (Turner & Corlett 1996).
17 However, small forest patches in fragmented landscapes may prevent the successful immigration
18 of dispersing individuals (Gustafson & Gardner 1996; Haynes *et al.* 2007). Clearly, if animals
19 are unable to move between the habitat patches, the ecological benefits of immigration and the
20 rescue effect will not be realised (Howe, Davis & Mosca 1991).

21

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12

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1 Table 1. Landscape variables describing the composition and modification of local (12.6 km²)
 2 landscapes for the dispersal and occupancy study areas, and the composition and configuration of
 3 between-population (0.5 km-wide) landscapes for the dispersal study area. The table includes
 4 the variable names, descriptions, and means (ranges) for continuous variables or levels
 5 (frequencies) for categorical variables.

Landscape variables	Descriptions	Means (ranges) or levels (frequencies)
Local landscapes		
Forest type	Rainforest type of the sampled locations within the landscapes.	Upland (3), Lowland (7) ^a Upland (15), Lowland (31) ^b
Rainforest cover	Percent of rainforest cover within the contemporary landscapes.	41.6 % (10.8 – 93.6 %) ^a 27.3 % (0.5 - 84.7 %) ^b
Rainforest cover lost	Percent change of rainforest cover for historic and contemporary landscapes.	24.8 % (1.8 – 53.7 %) ^a 36.8 % (0.0 - 97.2 %) ^b
Patch size lost	Percent change of mean rainforest patch size for historic and contemporary landscapes.	62.0 % (11.5 – 94.6 %) ^a 64.2 % (0.0 – 98.9 %) ^b
Patch structure		
Patch area	The natural log of the area of the rainforest patch.	31.9 km ² (<0.1 - 427.5 km ²) ^b
Mean patch isolation	Mean distance to the nearest rainforest patch in each quadrant of the four cardinal directions.	1.2 km (0.1 - 6.8 km) ^b
Between-population landscapes		
Rainforest cover	Percent of contemporary rainforest cover within the landscapes.	40.9 % (7.7 – 98.9 %) ^a
Wet eucalypt forest cover	Percent of contemporary wet eucalypt forest	24.8 % (0.9 – 78.5%) ^a

	cover within the landscapes.	
Deforested land cover	Percent of deforested land cover within the landscapes.	18.0 % (0.0 – 50.3 %) ^a
Forest patch density	Density of contemporary forest patches within the landscapes.	8.2 km ⁻² (1.0 – 16.5 km ⁻²) ^a
Distance	Euclidean distance between the populations.	9.4 km (3.2 – 18.7 km) ^a

1 ^a Landscape variables for the dispersal study area.

2 ^b Landscape variables for the occupancy study area.

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1 Table 2. Model selection statistics for the effects of local landscapes and patch structure on
 2 logrunner patch occupancy, and the effects of local and between-population landscapes on
 3 emigration and immigration.

Model	K	$\log(L)$	AIC_c	ΔAIC_c	w_i
Patch occupancy					
$\psi(\text{Patch isolation} + \text{Rainforest lost}) p(\text{Forest type})$	5	-160.46	332.41	0.00	0.374
$\psi(\text{Patch isolation} + \text{Patch area lost}) p(\text{Forest type})$	5	-160.88	333.25	0.84	0.246
$\psi(\text{Patch isolation}) p(\text{Forest type} + \text{Time of day})$	5	-161.29	334.08	1.67	0.163
Emigration					
Patch area lost (local) + Rainforest cover (local)	6	-305.49	623.80	0.00	0.171
Patch area lost (local)	5	-306.92	624.42	0.62	0.125
Patch area lost (local) + Forest type (local)	6	-306.01	624.83	1.03	0.102
Patch area lost (local) + Patch density (between)	6	-306.40	625.61	1.81	0.069
Patch area lost (local) + Distance (between)	6	-306.53	625.87	2.07	0.061
Patch area lost (local) + Rainforest lost (local)	6	-306.61	626.03	2.23	0.056
Patch area lost (local) + Rainforest cover (between)	6	-306.92	626.64	2.84	0.041
Patch area lost (local) + Deforested cover (between)	6	-306.91	626.64	2.84	0.041
Patch area lost (local) + Wet eucalypt cover (between)	6	-306.92	626.66	2.86	0.041
Rainforest lost (local)	5	-308.18	626.93	3.13	0.036
Forest type (local)	5	-308.27	627.11	3.31	0.033
Rainforest lost (local) + Forest type (local)	6	-307.49	627.79	3.99	0.023
Immigration					
Patch area lost (local) + Patch density (between)	6	-305.33	623.47	0.00	0.241

Rainforest lost (local) + Patch density (between)	6	-306.44	625.69	2.22	0.079
Patch area lost (local) + Rainforest cover (between)	6	-306.53	625.87	2.40	0.073
Patch area lost (local)	5	-308.17	626.91	3.44	0.043
Rainforest lost (local) + Rainforest cover (between)	6	-307.14	627.09	3.62	0.039
Patch area lost (local) + Wet eucalypt cover (between)	6	-307.15	627.11	3.64	0.039
Forest type (local) + Patch density (between)	6	-307.20	627.20	3.73	0.037
Patch area lost (local) + Deforested cover (between)	6	-307.33	627.46	3.99	0.033

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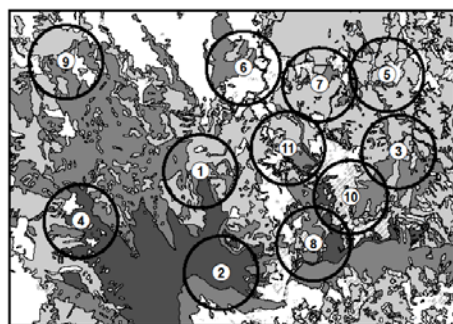
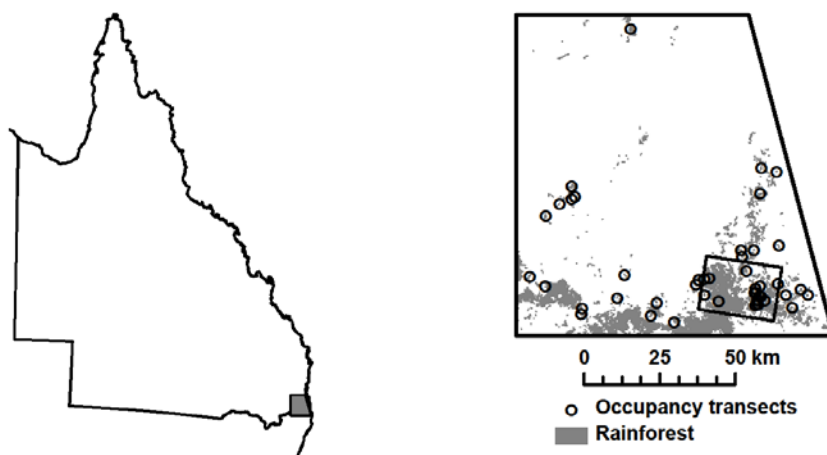
1 Table 3. Parameter estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95%
 2 confidence limits from the best approximating models for the effects of local landscapes and
 3 patch structure on logrunner patch occupancy, and the effects of local and between-population
 4 landscape features on emigration and immigration.

Parameters	Estimate	SE	LCL	UCL
Patch occupancy				
ψ (Intercept)	2.384	0.924	0.573	4.196
ψ (Patch isolation)	-2.683	1.049	-4.738	-0.627
ψ (Rainforest lost)	-1.701	0.770	-3.210	-0.192
p (Intercept)	-0.688	0.188	-1.056	-0.320
p (Upland forest)	0.917	0.283	0.362	1.472
Emigration				
Intercept	12.820	1.142	10.185	15.454
Patch area lost (local)	-0.050	0.014	-0.079	-0.022
Rainforest cover (local)	0.029	0.016	-0.003	0.061
Random effect of emigration population	0.055	0.933	0.000	3.292
Random effect of population pair	3.166	2.919	0.000	9.424
Residual error	12.235	3.396	7.449	18.586
Immigration				
Intercept	10.348	1.635	6.650	14.047
Patch area lost (local)	0.056	0.020	0.016	0.097
Patch density (between)	-0.353	0.148	-0.651	-0.056
Random effect of immigration population	2.056	1.502	0.104	7.707

Random effect of population pair	5.133	2.297	0.775	10.540
Residual error	9.510	2.133	6.324	15.307

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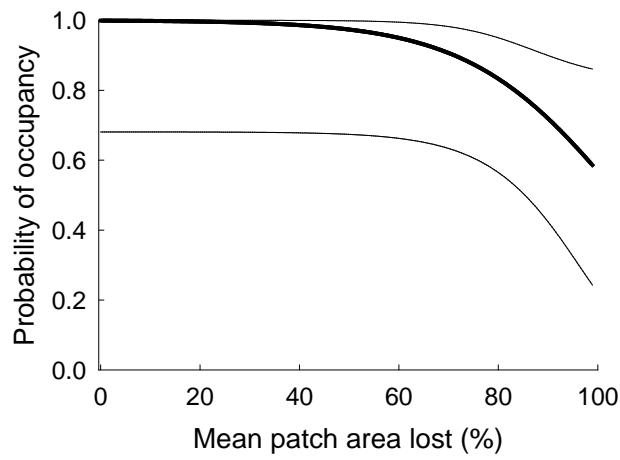
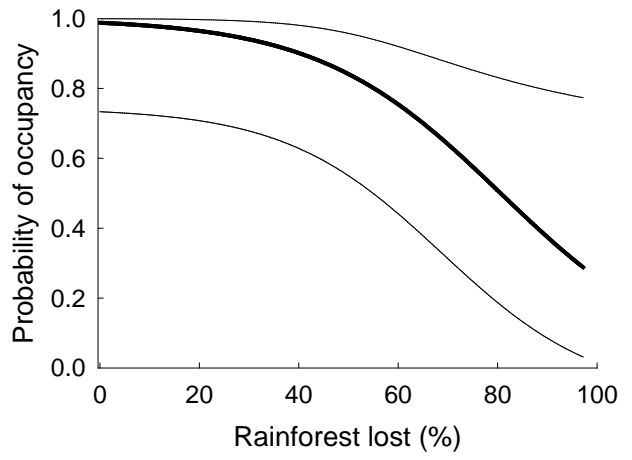
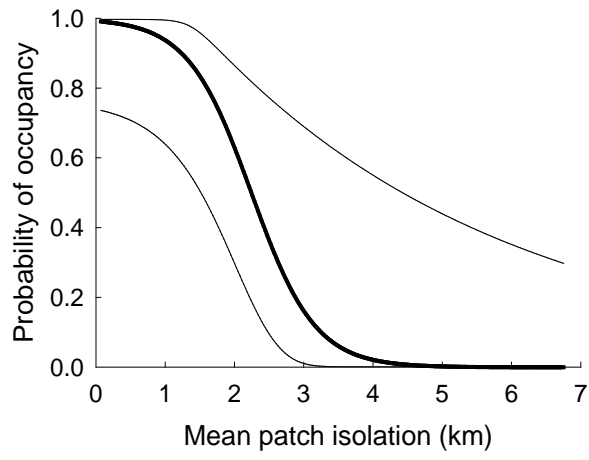
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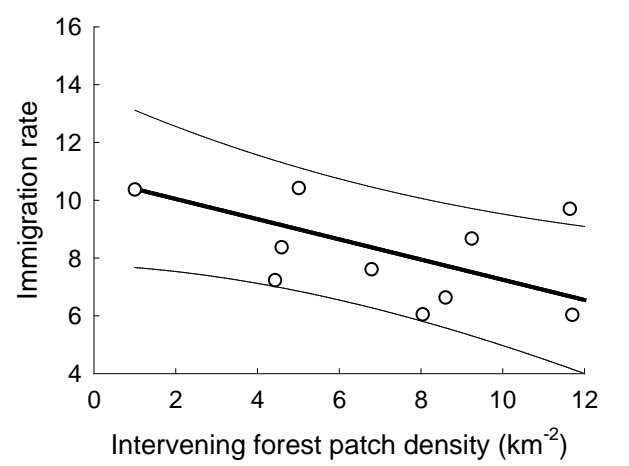
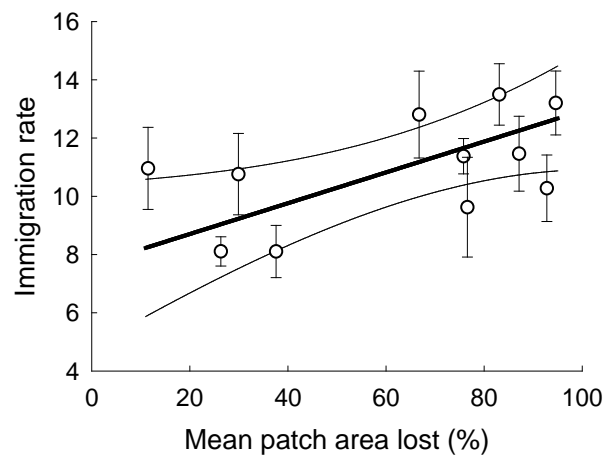
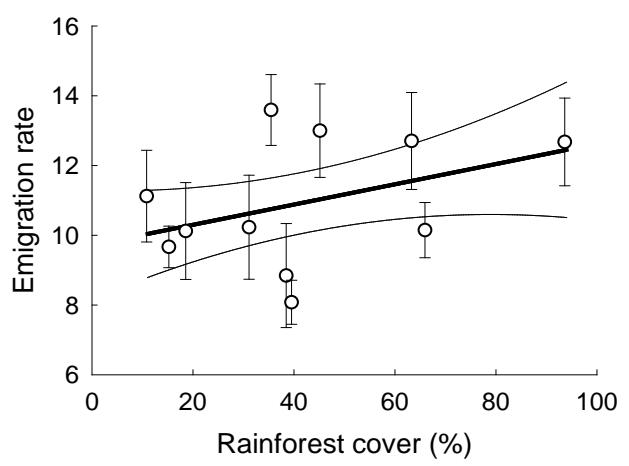
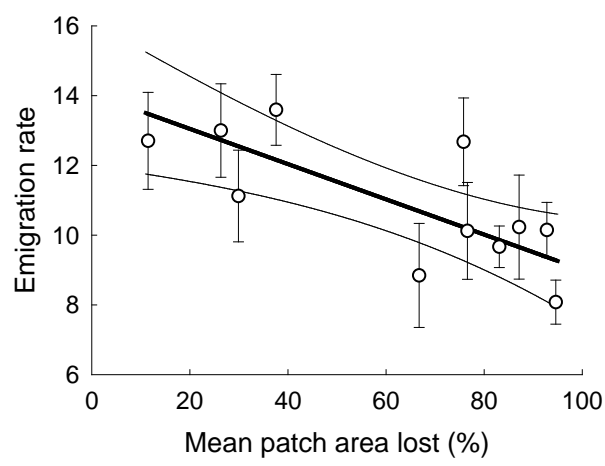
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1 **Figure legends**

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3 Figure 1. Map of the regional and dispersal study areas in South East Queensland, Australia.

4 The map of the regional study area depicts the location of the occupancy transects and the

5 distribution of rainforest vegetation. The map of the dispersal study area shows the current

6 landscape structure and landscape buffers for the 1) Binna Burra, 2) Coomera River, 3) Fairview

7 Mountain, 4) Green Mountains, 5) Mount Nimmel, 6) Nixon Creek, 7) Numinbah Valley, 8)

8 Quamby Falls, 9) Sarabah, 10) Warrie and 11) Willowie logrunner populations.

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10 Figure 2. Predicted logrunner patch occupancy as a function of mean patch isolation and

11 rainforest lost from the best approximating model, and mean patch area lost from the second best

12 approximating model. The bold trend lines are model averaged probabilities of occupancy and

13 the filled areas are unconditional 95% confidence intervals.

14

15 Figure 3. Predicted logrunner emigration as a function of mean patch area lost and remnant

16 rainforest cover in local landscapes and predicted logrunner immigration as a function of mean

17 patch area lost in local landscapes and forest patch density in between-population landscapes.

18 The bold trend lines are model averaged emigration and immigration rates and the filled areas

19 are unconditional 95% confidence intervals. The open circles are mean emigration and

20 immigration rates for each population and the error bars are one standard error of the mean. The

21 open circles without error bars are the immigration rates for the Binna Burra population.