Functional connectivity and landscape genetics of Box–Ironbark birds

John Nevil Amos

BA (Hons.) Oxford University, MSc (Conservation) University College London.

A thesis submitted in total fulfilment of the requirements

for the degree of Doctor of Philosophy

November 2014

School of Biological Sciences

Monash University

Australia

COPYRIGHT NOTICES

I dedicate this work to my parents: my dad, who first kindled my interest in natural history and the pursuit of knowledge for its own sake; and my mum who, always encouraged me to pursue my interests. I wish they were here to see this finally finished 26 years after I headed down under for a few years postgrad study.

Superb Fairy-wrens (*Malurus cyaeneus*)

TABLE OF CONTENTS

FIGURES

TABLES

ABSTRACT

Habitat loss, fragmentation and degradation are drivers of major declines in biodiversity and species extinctions. The actual causes of species population declines following habitat change are more difficult to discern. In this thesis I attempt to identify, based on published data on mobility and their ecological responses to fragmentation, some of the processes that may have led to patterns of decline for 10 woodland-dependent birds in fragmented woodlands of central Victoria, Australia. Eight species had been identified as 'decliners' (species that disappear from suitable patches when landscape-level tree cover falls below species-specific thresholds) and two as 'tolerant' species (whose occurrence in suitable habitat patches is independent of landscape tree cover).

I investigated the contribution of decreased structural connectivity on functional connectivity as a cause of the observed declines. A set of landscape connectivity models was constructed of each species covering a range of plausible values. The two dominant algorithms for summarising effective distances used in modelling complex fragmentation patterns in landscape genetics—least-cost path and circuit distance—were used to construct these models The results of the two methods were compared and circuit distance was determined to be the more appropriate approach for use in my study system. Choice of algorithm and null model were important influences on inferences in landscape genetics.

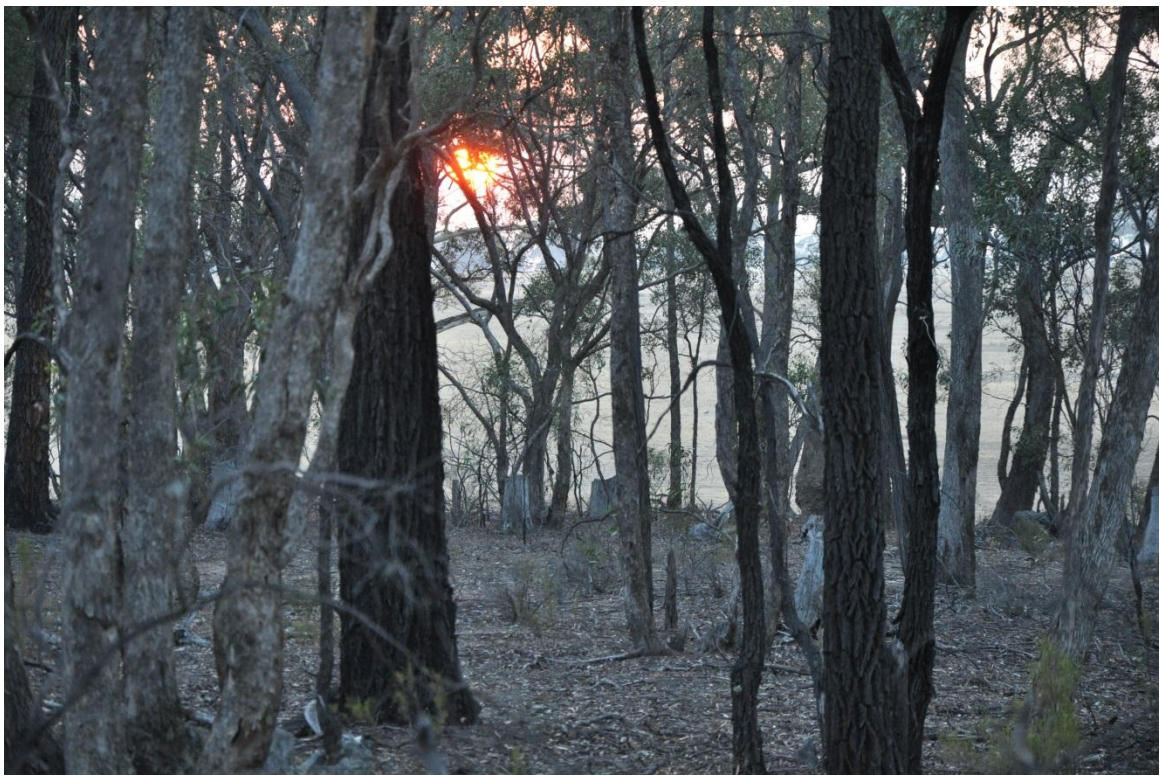
I predicted (1) fragmentation would impede dispersal and gene flow of 'decliners' but not of 'tolerant' species; and that fragmentation effects would be stronger (2) in the least mobile species, (3) in the more philopatric sex and (4) in the more fragmented region. These predictions were then tested with a large empirical genetic dataset (2198 individuals from 63 sites across a 170 × 50-km study area). I fitted models specific to sex and geographic zone in order to account for sex-biased dispersal and potential scale- and configuration-specific effects.

As expected, four of the least mobile decliners showed reduced genetic connectivity. Responses were sex specific in the two least mobile species. The tolerant species and (unexpectedly) four of the more mobile decliners showed no reduction in gene flow. Weaker genetic effects were observed in the geographic zone with more aggregated

vegetation, consistent with gene flow being unimpeded by landscape structure. These results indicate that, excepting the most sedentary species in our system, the movement of the more dispersive sex maintains overall genetic connectivity across fragmented landscapes in the study area.

I examined relationships among configuration, extent and status of native vegetation and three commonly used indicators of individual body condition and chronic stress in 13 species, two measures of changes to population processes (sex ratio and individual homozygosity) in 10 species and allelic richness in five species. Little support for relationships between site or landscape characteristics and individual or population response variables was found.

These findings, along with related work to which I contributed, but that does not form part of the thesis, highlighted the need for management to increase both connectivity, for the least mobile species, and critical resource availability for other species to conserve these declining species.



A Box-Ironbark forest remnant.

GENERAL DECLARATION

In accordance with Monash University Doctorate Regulation 17.2 Doctor of Philosophy and Research Master's regulations the following declarations are made.

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes three original papers published in peer-reviewed journals and one unpublished manuscript. The core theme of the thesis is investigation of the effects of landscape fragmentation on a suite of woodland birds. The ideas, development and writing of all the papers in the thesis were the principal responsibility of me, the candidate, working within the School of Biological Sciences under the supervision of Paul Sunnucks and Ralph Mac Nally.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers, and acknowledges input into team-based research. Field sampling for the project involved a major coordinated team-based effort with a field team leader/technical officer (initially Alan Lill, then Naoko Takeuchi) responsible for much of the logistics of preparation for field trips. I was a principal member of the field team for approximately 80% of field sampling, and was responsible for identification of suitable sampling sites for much of the time. I gained my A-class Australian Bird and Bat Banding Scheme license as early as possible in the project and was then able to supervise other team members. In addition to the project members who are all co-authors on one or more of the papers below, the field sampling effort required the assistance of a large number of volunteer assistants.

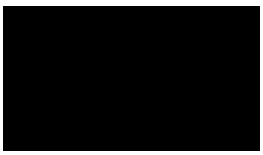
I was not involved in the laboratory work to genotype and sex birds, which was an essential input to the analyses in Chapters 3, 4 and 5. That work was undertaken by several of the co-authors led by Sasha Pavlova, and identified in the individual declarations at the start of Chapters 4 and 5.

In the case of Chapters 2, 4 and 5 my contribution to the work involved the following:

Thesis Chapter	Publication title	Publication status*	Nature and extent of candidate's contribution
2	Predicting landscape genetic consequences of habitat loss, fragmentation and mobility for multiple species of woodland birds	Published as: Amos, J. N., A. F. Bennett, R. Mac Nally, G. Newell, J. Q. Radford , A. Pavlova, J. Thompson, M. White, and P. Sunnucks. 2012. Predicting landscape genetic consequences of habitat loss, fragmentation and mobility for multiple species of woodland birds. PLoS ONE **7**:e30888.	Manuscript preparation, development of detailed experimental design and approach, geographical information system analysis and production of landscape models, genetic and statistical analyses, development of key concepts and conclusions
4	Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds	Published as: Amos, J. N., K. A. Harrisson, J. Q. Radford, M. White, G. Newell, R. M. Nally, P. Sunnucks, and A. Pavlova. 2014. Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds. Ecology **95**:1556-1568.	Manuscript preparation,collection of genetic samples as principal member of field team, formulation of modifications to statistical approach, performance of statistical analyses, formulation of discussion and conclusions
5	Little evidence that condition, stress indicators, sex ratio, or homozygosity are related to landscape or habitat attributes in declining woodland birds	Published as: Amos, J. N., S. Balasubramaniam, L. Grootendorst, K. A. Harrisson, A. Lill, R. Mac Nally, A. Pavlova, J. Q. Radford, N. Takeuchi, J. R. Thomson, and P. Sunnucks. 2013. Little evidence that condition, stress indicators, sex ratio, or homozygosity are related to landscape or habitat attributes in declining woodland birds. Journal of Avian Biology **44**:45-54.	Manuscript preparation,, collection of morphometric and haematological data as principal member of field team, performance of genetic and statistical analyses, formulation of discussion and conclusions

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Signed:



Date: **12/11/2014**

ACKNOWLEDGEMENTS

I would like to thank:

- My supervisors Paul Sunnucks and Ralph Mac Nally for their insight and patient assistance throughout. Thanks in particular to Paul, who encouraged and coaxed me over several years, then made the opportunity available, for me to return to study for a PhD after many years of absence from fieldwork and academia: I hope he does not regret it. If nothing else he was able to get his revenge for a split infinitive back in 1985. Thanks also to my additional *de facto* supervisor Sasha Pavlova for her continuous encouragement and many lengthy discussions initiating me gently into the mysteries of population genetics.
- My co-authors, Peter Arcese, Andrea Taylor and six anonymous reviewers of the papers that form part of this thesis for comments that greatly improved the quality of the publications and for their support, encouragement and access to their datasets.
- Andrea Taylor for final proof editing of the thesis.
- Garry Cheers, Rohan Clarke, Doug Robinson and Chris Tzaros, for provision of estimates of mobility of bird species, and Philip Chan for assistance with running simulations on the Monash Sun Grid: they provided their expertise allowing me to develop the expert-opinion-based models for Chapter 2.
- Geoff Sutter, who did the 'habitat hectare' assessments of all our sites.
- Erin Landguth, Brian Hand and Brad McRae, for discussions of ideas about patterns of isolation-by-resistance, and Erin and Brian for assistance with CDPOP simulations of our landscapes.
- Veronica Doerr and Eric Doerr, for provision of data and valuable discussion on dispersal movements and gap crossing in Brown Treecreepers and a number of other species.
- Andreas Svenson and particularly Jim Thomson for assistance and discussion of statistics and R, and writing of WinBugs scripts for me.
- Naoko Takeuchi, bird bander and fieldworker extraordinaire for her enthusiasm, drive and organisation keeping the fieldwork going, making sure we always had a supply of chips, and for teaching me how to make ma-po tofu.

- The other members of the field team: Alan Lill, Katherine Harrisson, Linda Grootendorst, Bec Bray, Shandiya Balasubramaniam and all of our volunteer field assistants—Anne Hughes, Anton Polesskiy, Archana Sharma, Adrian Martins, Alana Hallinan, Alexander Zelikin, Alice Taylor Sunnucks, Anastasia Polesskiy, Andrea Taylor, Anton Polesskiy, Ashley Herrod, Brigitte Stadler, Chelsea Eaw, Craig Gaston, Darcy Radford, David Pay, Emma Carlos, Eric Doerr, Fiona Bowie, Glenise Moore, Graham Stone, Grazyna Garbowski, Heidi Miller, Helen Lowry, Ira Mark, Irina Beme, Jason Jones, Jim Radford, Jingle Fan, Joachim Brindeau, John Land, Jolene Scoble, Julia Deleyev, Julie Whitfield, Kate Richardson, Kate Stevens, Laura Stenzler, Lindsay Tyler, Maree Mckinley, Maria Goretskaia, Marian Weaving, Mark Mackinnon, Martine Maron, Masha Roitman, Mathew Berg, Matt Landy, Megan Price, Michael Hanssen, Michelle Basset, Naoki Onishi, Niclole Bullen, Pam Amos, Pam Land, Peter Jenkins, Prue Write, Raoul Mulder, Rob Moore, Roger Standen, Rowan Amos, Ruby Taylor Sunnucks, Stephanie Tyler, Susan Wood, Tanya Hardiman, Terry Korodaj, Thanh-Lan Gluckman, Vanessa Keogh, Veronica Doerr and Wengi.
- The lab team led by Sasha, who undertook the arduous task of genotyping so many birds. Without this work my thesis would have been impossible. This small acknowledgement does not do justice to the enormity of their task.
- My office mates at Monash: Greg, Gillis, Val, Megan, Jo, Darren and Amber, for friendly encouragement and chats over tea and coffee and beers at the Nott.
- Parks Victoria, and Department of Sustainability and Environment for granting access to Parks and State forest land, and to the private landholders—Andrew Hutchinson, Anne Hughes, Bob Passalick, Colin Patterson, Craig Gaston, David O'Connor, David Pay, Gloria Silas, Heather, Jo and Phil Lemin, John Williamson and Alison Tease, Lindsay Bray, Pat Andruchow, Rob Swanton, Rosalie Burgess and Tony Easton—who allowed us to work on their properties, and in one case to capture pardalotes nesting in the walls of their house!
- The Holsworth Trust, for generous funding for purchase of pardalote nestboxes and funding my attendance at the International Congress for Conservation Biology in Edmonton. Birds Australia (now Birdlife Australia) for their generous contribution that supplemented my scholarship. Department of Sustainability and Environment, Museum of Victoria, Department of Primary Industries, Parks Victoria, North Central Catchment Management Authority, Goulburn Broken

Catchment Management Authority, Birds Australia, Australian National Wildlife Collection who were our partners on Australian Research Council Linkage Project LP0776322 that funded the main project.

- The Australian Bird and Bat Banding Scheme and individual bird banders who agreed to make their banding data available for my use.
- My family—Pam, Elowen and Rowan—from whom I was absent far too frequently on fieldwork or in the office, for far too many years: for putting up with my absent-mindedness and even-grumpier-than-usual nature when progress of the thesis was not good.
- Lastly, the birds and the remaining bush, for the solace and joy they provide me, hoping that in some small way this work assists their conservation; for their own sake and for the enjoyment of future generations

 .

Striated Pardalote (*Pardalotus punctatus*)

1. INTRODUCTION

Clearing and modifying native habitats for human use is a major cause of biodiversity decline (Fahrig 2003). The negative effects of habitat loss may be exacerbated by interrelated changes including reduced connectedness of remnant patches of originally contiguous populations and increased probability of stochastic processes causing local extinction from patches as a result of smaller population size (Lindenmayer and Fischer 2006). Modification of habitat quality of remnants through increased edge effects and more intensive human use of remnants (Lindenmayer and Fischer 2006) may decrease the carrying capacity of those areas. Alternatively, reduction in habitat quality sometimes leads to increased stress and decreased individual condition of surviving organisms (Mazerolle and Hobson 2002, Suorsa et al. 2003a).

Whereas the pattern of decline in populations of many species through loss and change of habitat is well known (Fahrig 2001, Lindenmayer and Fischer 2006), the causal processes have often been harder to pin down. Responses to habitat fragmentation vary between species (Mönkkönen and Reunanen 1999, Bennett and Radford 2009), and the covariation of underlying factors has made it difficult to separate causal drivers (Lindenmayer and Fischer 2007). Nevertheless, to ameliorate current biodiversity declines it is imperative that we identify causation so that conservation management can be effectively directed.

As habitat becomes fragmented (i.e. broken apart into smaller units separated from each other by less-suitable habitat), mobility of individuals and population connectivity among sub-units of the original population may be impeded. Where fragmentation is caused by clearance of native vegetation such as forest or woodland, loss of structural connectivity is the most apparent impact. Structural connectivity is an attribute of the physical configuration of habitat patches relating to their degree of contiguity within the cleared matrix. Metrics of structural connectivity gained traction for use in management decisions because they are relatively easy to quantify (Lindenmayer and Fischer 2006). However, measures of structural connectivity are most useful where they inform our understanding of functional connectivity, such as the ability of individuals to move or disperse among areas of remnant habitat (Merriam 1984, Taylor et al. 1993).

Functional connectivity is dependent on the effect that landscape structure and landscape elements (such as the extent and organisation of remnant vegetation in woodland systems)

have on the dispersal ability of an organism, its response to changed land cover and to novel features of environments, and other aspects of ecology and life history (Baguette and Van Dyck 2007, Doerr et al. 2014). Functional connectivity among remnants requires not only that individuals can disperse among patches, but that there is successful reproduction of migrants, resulting in gene flow (Doerr et al. 2014).

The most widespread approaches to spatially explicit modelling of population connectivity in heterogeneous landscapes have made use of raster-based maps representing land cover classes or landscape features (Spear et al. 2014). Calculations of the modelled connectivity between points across the landscape surface can be made by assigning a value to the relative difficulty of crossing a raster cell given its classification, and evaluating the aggregate difficulty of movement ('resistance distance') of an individual between the two points; an analogous approach can be taken with gene flow. Connectivity is the reciprocal of resistance. Several algorithms have been proposed for calculation of resistances. The most widely used approach has been the calculation of distances along the 'least-cost path' (LCP), that is, the route between two points that has the lowest sum of cell resistance values (Dijkstra 1959, Adriaensen et al. 2003). A second approach, 'circuit distance' (or CS, here), is now commonly used, in which the combined resistance of all possible routes between the points is calculated using electrical circuit theory (McRae and Beier 2007). LCP modelling has been criticised for making unrealistic biological assumptions, most importantly that the disperser has complete knowledge of its surroundings and is able accurately to choose the least costly path (Theobald, 2006, Baguette and Van Dyck, 2007). Alongside unrealistic assumptions, a second limitation of LCP is that, in its simplest form, it identifies only a single optimal route and does not accommodate the contribution of multiple possible routes to estimation of effective distance (Theobald, 2006). In contrast, CS allows for multiple paths, including some role for suboptimal ones. Despite these contrasts, the few studies that have compared the techniques have come to opposing conclusions about the accuracy of the methods in modelling functional connectivity (McRae and Beier 2007, Schwartz et al. 2009, Munshi-South 2012, Spear et al. 2014). A comparison of the two approaches for multiple species in the same landscape may help clarify the circumstances under which each performs best.

Modelled population connectivity must be compared to some independent estimate of connectivity. For most organisms and environments, realized connectivity at landscape

scales is very difficult to measure. However, population genetics approaches can help solve this challenge. The emerging discipline of 'landscape genetics' is concerned with the spatial arrangement of genetic variation in landscapes. The discipline combines population genetics, spatial statistics and landscape ecology. Through comparison of the spatial distribution of selectively neutral genetic markers (those best suited to estimating migration, gene flow and population history) with the spatial arrangement of habitat or other environmental variables across a landscape, inferences may be made regarding the patterns and mechanisms of individual movement and gene flow (Manel et al. 2003, Storfer et al. 2007). While landscape genetics is now a well-established discipline (Manel and Holderegger 2013), there is a need to extend the *post hoc* explanation of spatial genetic structures in single landscapes and species to a broader approach that allows predictions to be made for many species in an range of landscapes and scales (Balkenhol et al. 2009a, Segelbacher et al. 2010). The use of prior predictions of different landscape genetics responses expected in a range of species based on their individual ecology and behaviour is a way to progress this multi-species approach (Sunnucks 2011). This is possible, and perhaps most important where our understanding of the species dispersal ecology is poor (Shanahan and Possingham 2009). In this thesis, I take such an approach, testing the presence of landscape genetics fragmentation effects among a set of plausible landscape models by making prior predictions of the landscape model expected to be supported for each of 10 species of woodland birds with different dispersal abilities and previously estimated demographic responses to changes in landscape cover.

The case-study: birds of inland woodlands of south-eastern Australia

The woodlands and forest of south-eastern Australia have undergone broadscale clearance and degradation over the 200 years since European settlement, leaving only fragmented and degraded remnants of the original biome. The suite of birds dependent on these woodland habitats has undergone a major and continuing decline (Robinson and Traill 1996, Ford et al. 2001, Olsen et al. 2005, Ford 2011a). Multiple, interacting factors have contributed to this pattern, including absolute habitat loss, decreased ability to disperse through fragmented habitat, decreased quality of habitat remnants, increased competition with, or predation by, species that have become more abundant in remnant habitat as the result of edge effects, and climate change (Berry 2002, Piper and Catterall 2003, Mac Nally et al. 2009, Ford 2011a, Bennett et al. 2014).

Studies of woodland and forest-dependent birds in central Victoria have examined relationships between patterns of habitat fragmentation and species richness or likelihood of presence/abundance of certain taxa (Mac Nally et al. 2000, Radford et al. 2005, Radford and Bennett 2007, Thomson et al. 2007, Bennett and Radford 2009). In one of the first studies in which units of ecological replication were much larger than habitat patches, Radford et al. (2005) studied the effects of attributes of large 'landscapes' (10 × 10-km blocks) on the incidence of woodland-dependent birds *within sites of suitable remnant habitat in the landscape.* That is, they were seeking to encompass the influence at local scales of retaining a 'critical mass' of habitat at larger spatial scales. They concluded that the amount of tree cover remaining in landscapes was the single most important factor explaining variation of species richness, and that there was a threshold in landscape tree cover below which there was a precipitous decline in species richness in remnants. Within-landscape connectivity was significant, and the second most important factor in determining species richness (Radford et al. 2005).

In addition to species richness, in the same system, the response of individual woodland-dependent species to landscape-scale variables was investigated. Vegetation extent was the most frequent, and always positive, relationship with incidence of individual species. Any woodland-dependent species will necessarily show a decrease in absolute abundance with reduced landscape tree cover, since there will be less habitat remaining to occupy. Below a threshold level of tree cover, many species showed a *disproportionate* decrease in incidence in apparently suitable remnant habitat. These thresholds differed among species (Bennett and Radford 2009). In this thesis, I describe species that exhibited a disproportionate decline in incidence in remaining habitat relative to remnant tree cover as 'decliners', while those species whose incidence in remnant tree cover was independent of the amount of tree cover remaining in their total landscape were identified as 'tolerant'.

After habitat extent at the landscape scale, the next most frequent significant relationship was landscape configuration: increasing fragmentation had a negative effect on species incidence (Radford and Bennett 2007). This effect was much stronger for a smaller proportion of species.

The current thesis used landscape genetics to determine whether some of the observed decline in 10 species of woodland-dependent birds observed by Radford and Bennett

(2007) was due to loss of functional connectivity of birds among habitat remnants in the landscape. My work was carried out in a subset of the landscapes investigated by Radford and Bennett (2007). My study required genetic (blood) samples from population samples of the species of interest in each landscape, and so needed to be conducted in landscapes with levels of remnant tree cover above the thresholds identified in the earlier work, specifically those at which decliner species were likely to occur.

The e xtensive fieldwork required to obtain genetic samples also allowed the collection of haematological, morphometric and sex data. These data were used to test whether population declines in altered vegetation were contributed to by decline in health of individual birds associated with condition of remnant vegetation and the landscape context of habitat remnants. By framing the study to address these questions across 10 species with a range of known and expected responses to landscape tree cover, I strengthen the inferences that may be made, by allowing comparison and contrast of the responses of individual species.

Three chapters from this thesis have been published in international, peer-reviewed journals. They present a coherent approach to the questions outlined above. In Chapter 2 (Amos et al. 2012), I set out in detail the theoretical underpinnings, goals and experimental rationale of the research programme, along with the nature of the species and locations of the study system. That paper documents the classification of decliner and tolerant species according to their published response to landscape change, and what is known about their patterns of individual mobility and dispersal ability. A series of plausible landscape connectivity models is developed for each species, and between-site connectivity predicted using CS and LCP algorithms. Predictions of the best connectivity models for each species, based on relative mobility and response to landscape-level tree cover are made. Amos et al. (2012) sets up prior expectations for the study for testing with genetic data.

The two dominant models in connectivity modelling, LCP and CS may differ in suitability in different circumstances. Therefore, in Chapter 3 (unpublished) I compare the CS connectivity models with the LCP models, and compare the inferences made by each set of models. I discuss the importance of the selection of the appropriate null model in landscape genetics studies, and identify CS models as the most appropriate model set for use in testing the prior predictions made in Chapter 2.

Having identified CS as the better approach, I applied it in Chapter 4 (Amos et al. 2014) to test the prior predictions of the response of each of the 10 species to landscape fragmentation. I identified sex specific and possible scale and landscape configuration effects as additional factors complicating the predicted responses.

The outcomes of connectivity modelling showed negative effects of habitat loss and alteration on mobility and gene flow of one or both sexes of some species at some scales. However, compared to the foundational ecological work (Radford et al. 2005 and other papers in that programme), strong declines of nearly all species from the system requires explanations in addition to disruption to connectivity. Habitat quality and availability may affect fitness of birds within remnant vegetation patches. Therefore, in Chapter 5 I test for relationships among configuration, extent and condition status of native vegetation and three commonly used indicators of individual body condition and chronic stress in birds, as well as individual heterozygosity and allelic richness (AR) in each of the study species. Specifically, the aim was to determine whether habitat factors affected the health and fitness of individual birds to disrupt population processes, contributing to the patterns of decline observed by Radford et al. (2005), and Radford and Bennett (2007).

In the final chapter, (Discussion, Chapter 6), I draw together what this body of work has contributed to knowledge and approaches in the field, and note some potentially important forthcoming directions and opportunities in the rapidly developing discipline of conservation ecology.

Grey Shrike-thrush (*Colluricincla harmonica*)

DECLARATION FOR THESIS CHAPTER 2

Declaration by candidate

In the case of Chapter 2, the nature and extent of my contribution to the work was the following:

Nature of contribution	**Extent of contribution (%)**
Manuscript preparation, development of detailed experimental design and approach, geographical information system analysis and production of landscape models, statistical analyses, and development of key concepts and conclusions.	70

The following co-authors contributed to the work:

Name	**Nature of contribution**	**Extent of contribution (%) (for student co-authors only)**
A. F. Bennett	Contribution of design and analysis identifying species response to landscape tree cover and concept of decliner and tolerant species (Appendix A, supplementary material S1 in the published paper). Comment on manuscript	NA
R. Mac Nally	Co-supervisor, advice on statistical analysis, comment on manuscript	NA
G. Newell	Provision of spatial data for model development, comment on manuscript, Partner Investigator on funding research grant	NA
A. Pavlova	Contribution of detailed comments and discussion of manuscript and experimental design	NA
J. Q. Radford	Contribution of design and analysis identifying species response to landscape tree cover and concept of decliner and tolerant species (Appendix 1 supplementary material S1 in the published paper). Comment on manuscript, underlying experimental design, Principal Investigator on funding research grant	NA
J. R. Thomson	Advice on statistical analysis, comment on manuscript	NA
M. White	Provision of spatial data for model development, comment on manuscript, Partner Investigator on funding research grant	NA
P. Sunnucks	Principal supervisor, detailed comment on manuscript, development of underlying experimental design, Principal Investigator on funding grant	NA

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's signature	[redacted]	**Date** 12/11/2014
Main supervisor's signature	[redacted]	**Date 12/11/2014**

2. PREDICTING LANDSCAPE GENETIC CONSEQUENCES OF HABITAT LOSS, FRAGMENTATION AND MOBILITY FOR MULTIPLE SPECIES OF WOODLAND BIRDS

ABSTRACT

Inference concerning the impact of habitat fragmentation on dispersal and gene flow is a key theme in landscape genetics. Recently, the ability of established approaches to identify reliably the differential effects of landscape structure (e.g. land cover composition, remnant vegetation configuration and extent) on the mobility of organisms has been questioned. More explicit methods of predicting and testing for such effects must move beyond *post hoc* explanations for single landscapes and species. Here, we document a process for making *a priori* predictions, using existing spatial and ecological data and expert opinion, of the effects of landscape structure on genetic structure of multiple species across replicated landscape blocks. We compare the results of two common methods for estimating the influence of landscape structure on effective distance: LCP analysis and IBR. We present a series of alternative models of genetic connectivity in the study area—represented by different landscape resistance surfaces for calculating effective distance—and identify appropriate null models. The process is applied to 10 species of sympatric woodland-dependent birds. For each species, we rank *a priori* the expectation of fit of genetic response to the models according to the expected response of birds to loss of structural connectivity and landscape-scale tree cover. These rankings (our hypotheses) are presented for testing with empirical genetic data in a subsequent contribution. We propose that this replicated landscape, multi-species approach offers a robust method for identifying the likely effects of landscape fragmentation on dispersal.

2.1. INTRODUCTION

Habitat loss and fragmentation lead to small and increasingly isolated populations of wildlife in habitat remnants, and decreased metapopulation viability (Hanski et al. 1996, Hanski 1999, Hanski and Ovaskainen 2000).Small, isolated populations lose fitness through inbreeding depression of individuals and loss of genetic diversity from populations, decreasing adaptability to environmental change; these processes elevate extinction risk (Frankham and Ralls 1998, Saccheri et al. 1998, Frankham 2005). If the mean probability of extirpation in remnants exceeds the mean probability of recolonisation, then metapopulation extinction will eventuate. The time lag over which this occurs depends on many factors and may be many generations (Loehle and Li 1996). This 'extinction debt' is the number of taxa that, following habitat loss, no longer satisfy a threshold criterion for their survival (Hanski and Ovaskainen 2002). Thus many authorities (Crooks and Sanjayan 2006, Hilty et al. 2006) have identified the critical role of connectivity (the inverse of fragmentation) at landscape, regional and continental scales in effective conservation management.

An ongoing challenge is to tease apart the often interrelated ecological and genetic processes that result in biodiversity loss following habitat loss and alteration (Lindenmayer and Fischer 2006, Lindenmayer and Fischer 2007). Such knowledge is essential in order to design and implement management interventions to 'repay' extinction debt before species are lost (Szabo et al. 2011).

2.1.1. Landscape genetics approaches to assessing effects of habitat alteration

Landscape genetics (Manel et al. 2003) when combined with spatial modelling (Storfer et al. 2007) provides techniques for linking observed patterns of species occurrence to processes, particularly the relationships among structural and functional connectivity (Taylor et al. 1993, Taylor et al. 2006), genetically effective dispersal (Lowe and Allendorf 2010) and the maintenance of populations in fragments. Typically, landscape genetics studies have involved *post hoc* fitting of models to explain the relationship between genetic patterns and landscape structure. But this approach is limited in the robustness of its predictions, because alternative connectivity models are frequently correlated (Balkenhol et al. 2009a). Further, such models have usually been limited to inferences about a single species (Segelbacher et al. 2008).

A priori statements of explanatory models offer a more rigorous approach to linking observed pattern with process (Mac Nally and Bennett 1997, Martin and Possingham 2005, Balkenhol et al. 2009a). Replicate testing of predictions across multiple landscapes and species greatly strengthens inferences about population processes by testing generality (Segelbacher et al. 2010). The need for replication in landscape genetics studies has been emphasised in recent reviews (Holderegger and Wagner 2008, Balkenhol et al. 2009a, Short Bull et al. 2011). Inferences can be reinforced by concurrent examination of sympatric species predicted to have different responses to fragmentation on the basis of their known ecology and behaviour (Callens et al. 2011). This approach is valid even where relatively little is known about species attributes (Shanahan and Possingham 2009, Shanahan et al. 2010).

2.1.2. Modelling 'effective distance' for comparison with genetic data

Structural connectivity is an attribute of the physical configuration of suitable habitat patches within a landscape. Functional connectivity is an emergent property of individual species–landscape interactions (Taylor et al. 2006). It has been defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al. 1993), and thus reflects the effect that landscape structure and different landscape elements have on the dispersal ability and gene flow of an organism (Coulon et al. 2004, Coulon et al. 2006, Baguette and Van Dyck 2007)

The most widely adopted approach to estimating the relationship between structural and functional connectivity is to model 'effective distance', the 'Euclidean distance modified for the effect of landscape and behaviour' (Adriaensen et al. 2003) on the dispersal of an organism between locations in the landscape. Effective distance can then be compared with dissimilarity or distance measures, such as genetic distances between populations or individuals, or estimates of numbers of dispersers between habitat patches in a landscape.

Effective distance may be modelled by using LCP algorithms (Dijkstra 1959, Adriaensen et al. 2003). These account for differing costs (resistance per unit distance) of passing through different landscape elements. The algorithms identify the path through a landscape that minimises the resistance to an organism moving between two points, and thus calculate the least-cost distance. Such information on potential paths through the landscape, correlated with estimates of functional distances or dispersal (e.g. genetic

distances or observed dispersal events from mark–release–recapture or radiotelemetry), is often used to estimate the role of landscape structure as a constraint to dispersal (Broquet et al. 2006, Epps et al. 2007, Walker et al. 2007, Lada et al. 2008a).

LCP modelling has been criticised for its biologically unrealistic assumptions, such as that the disperser has complete prior knowledge of its surroundings and on this basis chooses the least costly path (Theobald 2006, Baguette and Van Dyck 2007). Another perceived drawback is that simple LCP analysis identifies only a single optimal route, rather than the contribution of multiple possible routes to effective distance (Theobald 2006), and so may not represent gene flow that accumulates across multiple dispersal events over time. Despite its limitations, LCP modelling has consistently shown predictive value when tested with molecular genetics data and compared with dispersal paths derived from radiotelemetry (Driezen et al. 2007)

Extensions of LCP methods may partially overcome some of these limitations by allowing the mapping of near-optimal or multiple pathways (Theobald 2006, Cushman et al. 2009, Pinto and Keitt 2009). The isolation-by-resistance (IBR) model of McRae (2006), also based on calculations of movement costs across a resistance surface, is becoming more widely adopted (Sunnucks 2011). IBR offers a conceptual model in which landscape resistance is the analogue of electrical resistance, and the movements of individuals and flow of genes are analogues of electrical current. It greatly extends the ability to model multiple complementary paths of connectivity, while being sufficiently computationally efficient to allow its use over large landscapes at relatively fine resolution (e.g. grids of 10^8 cells) (McRae et al. 2008). The associated software, Circuitscape (McRae and Shah 2009), generates maps of current (an analogue of gene flow or dispersal density) that indicate potentially important areas for maintenance of, or constraints to, functional connectivity.

IBR was found to explain a greater proportion of variance in genetic population structure than IBD or least-cost distance in simple model networks and when dealing with species ranges at (sub) continental scales (McRae 2006, McRae and Beier 2007). At least one other study found that least-cost distance explained a greater proportion of genetic variation than circuitscape distance; however, the resolution of the grids used in the two calculations was different (Schwartz et al. 2009). The present study builds on this single

comparison of the two approaches by examining their performance across multiple species in the same landscapes.

Here, we construct a set of landscape resistance surfaces for use in modelling effective distance, to represent a number of alternative hypotheses about gene flow. This work forms part of a related large-scale empirical study in which we collected genetic data from 10 species of woodland bird, sampled at 65 sites across 12 landscapes (each 100 km^2) that differ in their extent and configuration of wooded native vegetation. In a subsequent contribution, we test these predictions generated from these gene flow hypotheses using empirical genetic data at two spatial scales: (1) relatively short distances *within* replicated landscapes; and (2) greater distances *across* the whole study area.

We take the approach advocated by Cushman and Landguth (2010) of incorporating multiple alternative hypotheses of genetic differentiation, ranging from no spatial structuring, through isolation-by-distance (IBD) (Wright 1943), to a number of alternatives representing heterogeneous landscape resistance. Based on these alternative hypotheses (represented by different resistance surfaces) we calculated effective distances between all sample collection sites, using two of the main methods for estimating effective distance: LCP analysis and IBR using Circuitscape (McRae et al. 2008). We also identify the appropriate null model representing IBD in a uniform landscape for each (Balkenhol et al. 2009b). Correlations between each effective distance model and the relevant null model are reported to emphasise potential challenges in distinguishing these effective distance models from pure IBD (Balkenhol et al. 2009b). For each target species, we rank *a priori* the expectation of fit of genetic response to the effective distance models according to the expected response of birds to loss of structural connectivity and landscape-scale tree cover. These expectations will later be tested using partial Mantel tests and 'causal modelling' (Legendre and Troussellier 1988, Cushman et al. 2006). Causal modelling is a technique to alternately condition each of two dissimilarity matrices using the other to examine the residual effect of each matrix on a third matrix in a series of Mantel and partial Mantel tests (Cushman et al. 2006).

Very different inferences about landscape resistance may result from resistance model tests in fragmented and unfragmented landscapes (Cushman et al. 2011). Our study design contains landscapes at three levels of fragmentation and varying levels of cover in fragmented landscapes for further exploration of this problem.

Several studies of landscape connectivity with both genetic data and individual tracking have used model selection between multiple landscape resistance hypotheses (Cushman et al. 2006, Shanahan et al. 2010, Shirk et al. 2010, Wasserman et al. 2010, Cushman et al. 2011). Some have strengthened their inferences by replication of landscapes, and one considered two species with contrasting habitat and *a priori* expectations of response to fragmentation (Shanahan et al. 2010). The multiple model selection approach reduces the probability of affirming the consequent (Cushman and Landguth 2010), where the range of plausible resistance hypotheses are incorporated in the models chosen. Landscape replication further reduces the chances of misleading correlations resulting from configuration of samples and landscape elements in a single landscape (Short Bull et al. 2011).

2.1.3. Woodland birds of the Box–Ironbark forests of central Victoria, Australia

The avifauna of dry woodland systems of southern Australia is experiencing continuing decline, due primarily to habitat loss compounded by a range of other contributory factors (Robinson and Traill 1996, Ford et al. 2001, Mac Nally et al. 2009). Radford et al. (2005) examined the incidence of 58 species of woodland-dependent bird in remnant tree cover in 24 landscapes, each 10 × 10-km in central Victoria. Below a threshold of c. 10% of native tree cover, there were steep declines in landscape-level species richness. Radford et al. (2005) interpreted this threshold in species richness as the terminal point of a series of species-level declines that commenced at much higher levels, c. 30–50%, of vegetation cover, indicating evidence of local payment of the extinction debt. There was much variation in the landscape attributes identified as most influential in predicting the incidence of individual species at the landscape scale and in the shape of individual species responses to landscape-level tree cover. About one-third of species showed no significant relationship between incidence in the landscape and level of tree cover, while other species showed a curvilinear response, indicating that these species' occurrences were declining more rapidly than expected given relative tree cover (Radford and Bennett 2007, Bennett and Radford 2009).

We examined current understanding of the mobility of 10 bird species to construct predictions of the effects of habitat loss and fragmentation. We constructed hypotheses about the extent to which the level of structural connectivity is reflected in changes in

functional connectivity that might be signalled by changed gene flow. In a subsequent paper we will test the predictions generated from these gene flow hypotheses using empirical genetic data, and examine some of the possible causes that may explain the pre-identified patterns of decline.

In summary, our intentions in this paper are to:

- Assemble and apply biological data and expert opinion to characterise the expected mobility of a suite of birds through different land cover classes in our study system.
- Formulate species-specific and spatially explicit prior models of gene flow (represented by pairwise effective distances), and rank them for each species, to yield explicit prior hypotheses of gene flow for subsequent testing with genetic data.
- Use and compare two predominant approaches to modelling effective distance (and hence connectivity), LCP analysis and IBR, including validation of the most appropriate null models for each.

2.2. MATERIALS AND METHODS

2.2.1. Ethics statement

Observation of birds was carried out under Department of Sustainability and Environment/Department of Natural Resources and Environment (DSE/DNRE permit numbers 10004294 and 10002099 under the *Wildlife Act 1975* and the *National Parks Act 1975*, DSE permit number NWF10455 under section 52 of the *Forests Act 1958* with approval and monitoring through Monash University ethics processes (BSCI/2007/07).

2.2.2. Study area

The study area is c. 10,000 km^2 of central Victoria in south-eastern Australia (Figure 1). The remnant native vegetation of the area is principally Box–Ironbark forest dominated by Grey Box (*Eucalyptus microcarpa*), Red Ironbark (*E. tricarpa*) and Yellow Gum (*E. leucoxylon*) on relatively infertile soils. Grassy forest and woodland containing *E. microcarpa*, *E. leucoxylon* and Yellow Box (*E. melliodora*) remnants occur on more fertile valley floors, with River Red Gum (*E. camaldulensis)* dominant along watercourses. These latter vegetation types were selected for pastoralism in the 1840s, and much of the landscape has been cleared of native woody vegetation for >100 years.

During the gold rushes of the 1850s–1860s, considerable logging and clearing of the native forests occurred and <2% of remaining forests are old growth (Environment Conservation Council 1997). Land clearing for agriculture followed, alongside timber cutting and firewood harvesting from 1870 to the Second World War and beyond (Environment Conservation Council 1997). Consequently, remnant forests and woodlands of the region are heavily fragmented, degraded and of low productivity. Only 19.2% tree cover remains in the study area (DSE 1990–1999). The intervening land is heavily cleared, though scattered trees remain in parts of the farmland (Environment Conservation Council 1997).

2.2.3. Landscape and site selection

Twelve 10 × 10-km landscapes were selected, nine of which were used by Radford et al. (2005). The present study aimed to identify processes leading to species declines. Therefore, all selected landscapes had tree cover above the 10% threshold proposed by Radford et al. (2005). The landscapes represented two tree cover configuration classes: 'dispersed' or 'aggregated' (Radford et al. 2005). Three other 'reference' landscapes were selected with the highest available extant tree cover (72–78%) to approximate continuous tree cover (Figure 1). Reference landscapes necessarily contain a high proportion of Red Ironbark forest, because of the selective clearance of vegetation types across the region (Environment Conservation Council 1997). Sample sites within these landscapes were chosen to be as similar as possible in local vegetation type to the fragmented landscapes.

All landscapes were composed of six land cover classes in varying proportions: native tree cover; plantation and horticulture; urban; unimproved pasture and native grassland; improved pasture; and arable land. The last three land cover classes were further subdivided according to presence or absences of scattered trees.

Within each landscape, three to six sites were selected for genetic sampling. Initial sites were chosen at the locations of transects used by Radford et al. (2005) in which there had been multiple incidences of the majority of the 10 target species (see below). The remaining sites were chosen to make possible the capture of a reasonable sample of the target species, and to provide a range of between-site distances.

2.2.4. Study species

Our study design compared 'decliner' species (i.e. those for which landscape-level incidence decreased disproportionately relative to landscape-level tree cover) with 'tolerant' species (i.e. those for which landscape-level incidence was proportionate to landscape-level tree cover). We analysed responses of 58 woodland-dependent species to landscape tree cover from data in Radford and Bennett (2007) to classify them as decliner or tolerant to decreasing area of tree cover (Appendix A, Table A1).

We then applied two filters to select a subset of these 58 species as study species. First, species had to be common enough in the study landscapes that there was a high likelihood of obtaining sufficient samples for genetic analysis from multiple sites. Second, we stratified species by assumed mobility from highly mobile to sedentary. Data to classify relative mobility were collated from the standard reference work on the avifauna of Australia (Higgins et al. 2001, Higgins and Peter 2002). These data collectively were used to categorise mobility subjectively for each species as sedentary, intermediate or mobile.

Ten study species were chosen (Table 1). These were two 'tolerant' species, White-plumed Honeyeater (*Lichenostomus penicillatus*) and Striated Pardalote (*Pardalotus punctatus*); and eight 'decliners'—Brown Treecreeper (*Climacteris picumnus*), Eastern Yellow Robin (*Eopsaltria australis*), Fuscous Honeyeater (*L. fuscus*), Grey Shrike-thrush (*Colluricincla harmonica*), Spotted Pardalote (*Pardalotus punctatus*), Superb Fairy-wren (*Malurus cyaneus*), Weebill (*Smicronis brevirostris*) and Yellow-tufted Honeyeater (*L. melanops*).

2.2.5. Construction of landscape resistance models

The geographic area used for spatial modelling was the minimum convex polygon enclosing all of the sample points, with a 25-km buffer surrounding this polygon added to minimise the increase of resistance values due to the grid boundary (Koen et al. 2010). We assigned a 'no data' value to cells outside of this area and excluded them from all calculations. All raster processing was carried out in ARCGIS version 9.3 (ESRI 1999-2008) and the results output to ASCII grid format using the Export to Circuitscape Tool (Jeness Undated). The scale of these raster data was chosen as the best compromise between the functional grain (Baguette and Van Dyck 2007) considered most relevant to

the birds (detectability of large individual trees and linear strips of tree cover requiring 10-m resolution), data availability and the size of the grid (hence computational load).

Landscape resistance surfaces were created as follows:
(1) *Null model surface*. Two null models were applied. One assumed that there is no spatial structure to genetic differentiation due to unrestricted gene flow at the scale of the study area. There is no resistance surface for this model, as spatially random genetic variability is expected. A second null model assumed homogeneous resistance—that is, the analogue of IBD (Wright 1943)—and for this model a raster with all cells having a resistance value of 1 was used. This surface allowed calculation of appropriate values that could then be used in partial Mantel tests to condition for the effect of geographic distance.

(2) *Surfaces based on tree cover*. A 10-m resolution raster of vegetation cover >2 m in height (DSE 1990–1999), essentially tree cover for the study area, is of sufficient resolution to allow identification of large, isolated trees and contiguous tree cover. The 10-m raster was generalised to 25 m (the finest scale at which all relevant datasets were available), such that any cell containing a 10-m-tree pixel was identified as tree cover. All cells of tree cover were allocated a value of 1 and cells with no tree cover were assigned a higher resistance value (2, 5, 10 or 100) to create four models of alternative resistance (Table 2). Models based on these surfaces were denoted TREE with a suffix for the resistance of the treed and non-treed area (e.g. TREE_1_5).

(3) *Surfaces based on habitat suitability derived from species distribution models*. The base data were represented by a 25-m raster of the predicted probability of occurrence of a species based on modelling presence records in relation to a range of spatially explicit environmental variables from satellite chrono-sequences, digital elevation models (for terrain and climate), and radiometric data (Liu et al. 2012). The continuous SDM outputs were transformed to produce a binary result (i.e. part of or not part of the distribution of the species) employing a default threshold that maximises the diagnosticity measure (Hilden 1991). Two models for each species with either high (10) or low (2) resistance for areas not classified as part of the species' distribution were constructed and are referred to by the species abbreviation with a suffix of 'HAB'.

(4) *Surfaces based on bird species mobility in land cover classes, predicted by expert opinion*. The dispersal behaviour of nearly all of the study species is poorly known, apart

from the Brown Treecreeper (Doerr et al. 2011) and Superb Fairy-wren (Mulder 1995). We therefore sought expert opinion on this. Five ornithologists with expert field knowledge of the birds of the study area were asked to estimate, for each of the study species, the probability that an individual bird, during its lifetime, would traverse distances of 100 m, 200 m, 500 m, 1 km, 5 km or 10 km of a given land cover class. The maximum value was 1 and the minimum permissible value was set at 0.0001. This was repeated for each of nine land cover classes identified in a modelled GIS land cover classification for the area (Sinclair SJ, White MD, Medley J, Smith E, Newell GR, unpublished manuscript). Two species (Spotted Pardalote and Striated Pardalote) were not included in the expert opinion elicitation because the decision to include them in the study post-dated the opinion survey.

In order to establish the among-expert variation in opinion, variance of estimates among experts and species as random effects were analysed. We used a linear mixed effects model and correlation of variance in the R package lmer4 (Bates et al. 2011), following (Czembor et al. 2011). Mean estimates of all experts for each combination of distance, land cover class and species were calculated and used as a mean probability of dispersal (i.e. landscape conductivity). The reciprocal of this conductivity value, the land cover class resistance, was to develop resistance surfaces and calculate effective distance for each species.

A 25-m raster of land cover classes was derived from satellite imagery (Sinclair SJ, White MD, Medley J, Smith E, Newell GR, unpublished manuscript), with further categorisation of cleared agricultural land with or without scattered trees. The final land cover classes were (i) native tree cover, (ii) plantation and horticulture, (iii) urban, (iv) unimproved pasture and native grassland, (v) improved pasture and (vi) arable crop. For the last three classes, all cells within a 50-m radius of a tree pixel and not in contiguous tree cover were denoted as scattered trees. These classes were assigned resistances according to the mean opinion of experts. Models based on these surfaces were denoted by the species abbreviation followed by EO (for expert opinion) and the distance for which conductivity was being estimated. For example, the model for Brown Treecreeper (BT) movement over 5000 m was denoted BT_EO_5000.

For all resistance surfaces, measures of effective distance between all 65 sampling points (Figure 1) were calculated with (a) the LCP approach, using UNICOR Version 1.0

(Landguth et al.); and (b) IBR using Circuitscape version 3.5.1 employing the pairwise resistance and connection between eight cells options (McRae 2006, McRae and Beier 2007).

The existence of artificial boundaries in raster surfaces used for calculating IBR leads to inflation of resistance estimates (Koen et al. 2010). Given that cells outside the model grid area were assigned an infinite resistance (McRae and Shah 2009), there will be an increase in pairwise resistance between points close to the edge of the grid. We also considered the shape of the relationship between resistance, least-cost and linear distance on a bounded grid in comparison to the expectations of IBD of either a linear or log-linear relationship with distance (Rousset 1997) again to inform null model choice.

2.2.6. Correlations among models

Landscape models of effective distance resulted in pairwise matrices for the 65 sample sites. These data (2080 pairwise comparisons) were non-independent: each 65 × 65-site matrix contained only 32 independent pairwise comparisons, the maximum possible without using a point twice. In order to compare alternative models while maintaining independence, correlation coefficients between landscape models were estimated by repeatedly sampling 32 randomly selected pairs for 1000 iterations of each of the pairwise distance matrices for each species and the tree cover model. Mean estimated R^2 and the 95% intervals for each model in comparison with the null models (IBD) were calculated. We used this approach rather than Mantel correlations because it provides an appropriate estimate of the true correlation among models conditional on the number of distinct data points (i.e. $N = 32$), rather than the much-inflated number associated with all pairwise correlations. Moreover, this bootstrapping technique provides an indication of potential variability in model correlations, which cannot be derived from the Mantel correlation. On the basis of this assessment, a subset of models including the appropriate null were chosen for ranking on prior expectation of their ability to predict genetic distances between sample sites (to be tested in a later paper explicitly linked to this one).

2.2.7. Forming the hypothesis: within-species ranking of the likelihood that landscape models will predict genetic data

Our models incorporate a range of heterogeneous landscape models implemented as IBR, and two null models: IBD, where individuals' mobility and gene flow are restricted by

geographic distance alone; and complete lack of significant spatial pattern at the scale of our study as individuals' mobility is unrestricted at the scale of the study area (i.e. panmixia). This last hypothesis is characterised by no significant effect of either IBR or IBD.

Based on existing knowledge for each species derived from the major reference work on the avifauna of the region (Higgins et al. 2001, Higgins and Peter 2002) (Appendix B), species response to tree cover change (tolerant or decliner) and expert opinion on species mobility, we ranked the models on their ability to predict genetic structure. These rankings of models for each species represent our hypotheses. We based our ranking on the following.

(1) The mobility of some species is sufficiently restricted to result in evidence of IBD at the scale of the study, whereas more mobile species are not expected to show this effect (i.e. sufficient individuals move throughout the study area and cause gene flow to result in drift connectivity (Lowe and Allendorf 2010) and there will be no spatial pattern in their genetic variability).

(2) We assume that habitat loss and fragmentation will reduce genetically effective dispersal between remnant tree cover, especially for low-mobility 'decliners'. If this proposition is correct, our model rankings are more likely to reflect the genetic data.

2.3. RESULTS

2.3.1. Development of landscape resistance models

2.3.1.1. Null models and Circuitscape edge effect

Values for pairwise least-cost distance and IBR (Circuitscape) across the study area when all grid cells had resistance equal to 1 (UNIFORM) were correlated with the geographic distance (GEOG) and with the log-transformed geographic distance (logGEOG). For least-cost distance on a uniform surface, the relationship with GEOG was strongest (R^2 = 0.998). For Circuitscape on a uniform surface (UNIFORM), over all pairs, correlation was also strongest with GEOG, but for pairs separated by less than 50 km it was more highly correlated with logGEOG (all pairs: R^2 = 0.97 and 0.89; pairs <50 km: 0.90 and 0.99 respectively). The cause of this complex curve is an 'edge effect' in Circuitscape, where pairwise resistances increase towards the edge of the grid. We demonstrated this 'edge effect' for a simplified simulated dataset (Figure 2) and for the more complex

pattern of our study area (not shown). This effect is disproportionately larger for greater pairwise distances at the same geographic distance from the grid edge (Figure 2). Consequently, for models based on least-cost distance, a suitable null model for comparison is simple geographic isolation (GEOG). For models developed using IBR (Circuitscape, CS), the most appropriate null model is CS_UNIFORM; that is, the model developed using Circuitscape with a uniform surface that also incorporates the edge effect.

2.3.1.2. Expert opinion models

Over all distances combined, the variation in mobility estimates (i.e. probabilities of traversing a given distance) among species was small (5% of variance in estimates) compared with variation among distances (28%), and was similar to variation among land use (9%) and experts (7%). When within-distance variation was considered, among-expert variance was the largest component of variance for distances ≤2 km (18–28%). At distances >2 km, land use and species were attributed the greatest proportion of variance.

There was a bimodal distribution of mean estimates of resistance. Mean estimates were either ≤23 (low resistance) or >2000 (high resistance) in each species. Mean resistance estimated for the three agricultural land covers without trees (i.e. unimproved pasture, improved pasture and arable land) were equal, as were crop and improved pasture with scattered trees. Therefore, the initial nine land cover classes were reduced to six resistance classes (Table 2).

The 'tolerant' White-plumed Honeyeater differed from all other species. The estimate of land cover resistance was low (<10) for up to 1 km for all land covers, and for all distances for all land covers except agricultural land without scattered trees. All other species submitted for expert opinion (all 'decliners') were estimated to have high resistance to movement (>2000) through land cover classes other than tree cover at distances ≥200 m.

The ranking of mean estimates by experts of movement ability through continuous tree cover was similar to the classification of dispersal abilities based on the literature (Appendix B). White-plumed Honeyeater, Yellow-tufted Honeyeater and Fuscous Honeyeater were estimated to have low resistance to movement up to 10 km, the maximum distance for which expert opinion was sought. For the other species, which we identified on the basis of the literature as poorer dispersers than the honeyeaters

(Appendix B), much higher resistance to movement through tree cover over 2 km or greater distances was estimated by the experts. However, within these poorer dispersers there was disagreement on ranking. Literature suggests that Brown Treecreeper was the least mobile, followed by Eastern Yellow Robin, Superb Fairy-wren and Grey Shrike-thrush. Expert opinion estimated Superb Fairy-wren and Eastern Yellow Robin to be the least mobile (high resistance at ≥2 km in tree cover). Brown Treecreeper, Grey Shrike-thrush and Weebill were estimated to have high resistance only at ≥5 km in tree cover.

We grouped the species according to information on their mobility summarised from the literature (Appendix B) and expert opinion. For some species, the available information was inconclusive; for example, the species may be described as generally sedentary but with anecdotal evidence of longer distance movements or vice versa. We classified all species into four groups (Table 1): sedentary/poor dispersers (Brown Treecreeper); species with inconclusive information that we considered were probably sedentary (Eastern Yellow Robin and Superb Fairy-wren); species with inconclusive information that we considered were probably of moderate or higher mobility (Spotted Pardalote, Grey Shrike-thrush, Striated Pardalote, Yellow-tufted Honeyeater and Weebill); and mobile species/better dispersers (Fuscous Honeyeater and White-plumed Honeyeater).

2.3.2. Correlations among models

All but three models with heterogeneous landscape resistances were correlated with GEOG, logGEOG, and CS_UNIFORM (estimated $R^2 > 0.5$, Appendix C). These three models (EYR_HAB_10, EYR_EO5000 and SFW_EO5000) had the highest mean resistances (i.e. lowest predicted gene flows). Least-cost distance models had a higher estimated mean correlation with GEOG (mean $R^2 = 0.95$) than did IBR models with any of GEOG, logGEOG or CS_UNIFORM (mean $R^2 = 0.73$, 0.74 and 0.67 respectively, Appendix C).

For White-plumed Honeyeater, Yellow-tufted Honeyeater and Fuscous Honeyeater, the low resistance (EO_100 and EO_200) expert opinion models were indistinguishable from IBD models ($R^2 \sim 1$, Appendix C). Therefore, EO_100 and EO_200 were not used for predictions. For the high resistance model set, we chose EO_5000, as resistances for this distance showed the most discrimination among species and the highest proportion of variance in estimates (41%, Table 3) due to the biologically pertinent factors of species and land cover.

2.3.3. Within-species ranking of models

Models were ranked, in the order of their predicted correlation with genetic distances, based on knowledge and expert opinion of the mobility and response to changed land cover for each species (Table 4, Appendix B). Highest correlation was ranked first and lowest correlation seventh. The ranking resulted in six hypotheses for the 10 species. The most sedentary decliners (Brown Treecreeper, Eastern Yellow Robin, and Superb Fairy-wren) were ranked similarly with high resistance models expected to provide best fit. Two moderately mobile decliners (Spotted Pardalote and Grey Shrike-thrush) were also ranked similarly. Weebill and Yellow-tufted Honeyeater were ranked similarly. Fuscous Honeyeater, the most mobile species, but a decliner, had an idiosyncratic response to landscape configuration: no IBD was predicted, but it may still show weak structure due to loss of connectivity in spite of its apparent mobility. The two tolerant species (Striated Pardalote and White-plumed Honeyeater) were not expected to have responses correlated with landscape heterogeneity. On balance, the information for White-plumed Honeyeater suggested that it may not be as highly mobile as the other honeyeaters and thus may show weak IBD. The information on mobility levels for Striated Pardalote was inconclusive, and therefore we ranked IBD and panmixia equally.

2.4. DISCUSSION

We made predictions about the likely genetic response of 10 bird species to the landscapes used in the study based on available data and on expert opinion. We grouped the 10 species into seven groups for expected response. Hypotheses were framed as the ranking of a series of landscape distance matrices (uniform resistance (IBD), and heterogeneous IBR/least-cost distance) plus no spatial structure for panmixia, for testing against genetic distances (Table 4).

We contend that the *a priori* ranking of a set of alternative landscape distance models based on available ecological information is a robust approach to testing landscape genetics hypotheses. This may be even more important in the light of problematically correlated landscape models and the risk of spurious correlations (Balkenhol et al. 2009a, Cushman and Landguth 2010). Ranking of multiple species adds generality. Prior predictions explicitly link characteristics of the organisms to their response to landscape structure (Segelbacher et al. 2010) and are considered to offer a more rigorous test of

inferences about ecological processes (Mac Nally and Bennett 1997, McIntire and Fajardo 2009).

2.4.1. Application of expert opinion and descriptive literature

The low variance in expert opinion among species suggests that experts believed that the loss of structural connectivity has a similar effect on the mobility of nearly all species. However, the White-plumed Honeyeater stood out as the exception as might be expected for the one tolerant species for which we had expert opinion. Some experimental evidence exists for the Brown Treecreeper, and to a lesser extent for Eastern Yellow Robin, White-plumed Honeyeater, Fuscous Honeyeater and Grey Shrike-thrush, that movement is constrained by cleared gaps of 100–200 m in tree cover, but may be facilitated by scattered trees in the intervening space (Robertson and Radford 2009, Doerr et al. 2011). This pattern was reflected in the expert opinion of relative mobility through land covers with and without scattered trees over a distance of 100 m for all species except the three honeyeaters.

Our assessments of the mobility of the different species were based on sparse datasets, mostly inferred from descriptive material and expert opinion. This enabled us to develop simple hypotheses that distinguish the expected landscape responses of a group of passerines found in the same general vegetation type but showing markedly different response to habitat loss.

Expert opinion was consistent with descriptive information from standard reference sources (Higgins et al. 2001, Higgins and Peter 2002) in the grouping of birds' mobility. However, it did not provide strong discrimination among most of the species in terms of response to structural connectivity. Gap-crossing behaviour may be similar for species that we have identified as having widely varying mobility (Doerr et al. 2011). If so, then our predictions of responses to heterogeneous tree cover would not be supported, and response to tree cover gaps should be similar in all woodland-dependent species. Our predictions of IBD, which are determined by general mobility rather than gap-crossing behaviour, would be unaffected.

Garrard et al. (2012) developed a model of natal dispersal based on feeding guild, wing length, mass and existing natal dispersal data reviewed from five studies of 84 species (mainly northern hemisphere) in 12 avian orders. The model was then used to predict

median natal dispersal distance for the species studied by Radford et al. (2005). A negative relationship was found between natal dispersal distance and the effects of habitat fragmentation on prevalence of a species in the landscape. This agreed with our predictions—that the effects of habitat fragmentation will be greater for poorer dispersers. However, the individual species identified as having the shortest natal dispersal distances by Garrard et al. (2012) are those identified here as the most mobile (the honeyeaters, *Lichenostomus* spp.). We believe this disagreement arises from the feeding guild classification of 'omnivore' being inappropriate for nectarivorous/insectivorous honeyeaters that are more prominent in the south-eastern Australia avifauna (Ford 1985) than in the Garrard et al. (2012) dataset.

2.4.2. Comparison among species and choice of null models

The consideration of multiple species allowed the ranked expectations per species to be contrasted. This offers additional inferences to the absolute fit of predictions to the sampling design, and has been highlighted as a way to enhance the usefulness of landscape genetics studies (Segelbacher et al. 2010).

The extent and scale of the grid for Circuitscape calculations is limited practically by computational capacity (memory and time) and data availability for land cover (Koen et al. 2010), and leads to grid 'edge effect' (Figure 2). The edge effect in Circuitscape computation enables IBR to account for complex range or habitat shapes in modelling of genetic differentiation (McRae 2006). However, where the Circuitscape grid has artificial boundaries that are imposed due to data or computational limits, this edge effect must be accounted for, and minimised through buffering (Koen et al. 2010). Therefore, we recommend the CS_UNIFORM distance as the null model (effect of IBD) for comparisons with other Circuitscape resistances when considering heterogeneous landscape connectivity, and particularly for use in partial Mantel tests. CS_UNIFORM distance most closely follows the predictions of IBD at multiple distances and in different habitat configurations (Rousset 2000, McRae 2006), and alleviates the inflation of resistances caused by artificial boundaries (Koen et al. 2010).

The shared basis of all the models of land cover classes, and principally tree cover, along with the relatively low resistance differentials, means that nearly all the models are correlated (Appendix C), making them difficult to distinguish among. The high level of correlations between plausible resistance models is near universal. Causal modelling

provides a robust methodology for comparison of, and selection among correlated distance hypotheses (Cushman and Landguth 2010), particularly when coupled with cross-conditioning of competing models (Wasserman et al. 2010). McRae (2006) argued that the value of the IBR model lies in its ability to examine the more subtle effects of dissimilar gene flow through different landscape components. Lower mean correlations between IBR compared to least-cost distance for the same resistance surfaces provides a greater level of discrimination in pairwise comparisons across complex landscapes than do least-cost distances. Therefore, for a given set of resistance estimates, an IBR model may be more readily distinguished from other models, and from IBD models.

2.4.3. Resistance values in this system compared with others

The resistance values identified here, with the exception of some of the expert opinion models (Table 2), are at the lower end of those published employing LCP (Coulon et al. 2004, Broquet et al. 2006, Stevens et al. 2006, Driezen et al. 2007, Walker et al. 2007) or IBD (Shirk et al. 2010). Some of these authors used values as low as 1:2 for their habitat: matrix ratio; 1:10 to 1:1000 were more usual, while 1:10,000 to 1:100,000 were used as barriers. The studies cited above all involved fragmentation impacts on mammals and amphibians. Birds may be expected to experience lower levels of landscape resistance because flight allows them to cross gaps more rapidly and to cover larger distances more efficiently than non-volant terrestrial vertebrates. The one recent study that used cost distance to examine landscape effects on passerine genetic structure used resistance ratios similarly low to ours (Shanahan et al. 2010). The extremes in those models varied from 1:2 to 1:4 in a least-path distance model.

Other multi-model selection studies have sought to maximise the explanatory power of the best model through a multi-step approach, first optimising the contribution of individual landscape elements, and then combining them (Shirk et al. 2010), or have combined inferences from extensive tracking data and to determine the most plausible landscape surfaces, which were then combined to produce a large number of combination models for a single species (Wasserman et al. 2010, Cushman et al. 2011, Wasserman et al. 2011). By making prior predictions between species comparisons using the qualitative data available on each, we have taken a different approach compared to previous studies to maximise the strength of our inferences. This approach is most useful where multiple species are sampled concurrently (e.g. such as mist netting of passerines), and where there

are not extensive data on individual movements, though basic descriptive natural history is available. The study system did not have the mountainous terrain, extreme climate and differentiation of forest types present in the previous studies of mammals in the mountains of the north-western USA (Cushman et al. 2006, Shirk et al. 2010, Wasserman et al. 2010, Cushman et al. 2011, Wasserman et al. 2011). The most similar approach to date (Shanahan et al. 2010) was also on forest birds, although that study was comparing the expected response of a habitat generalist with a specialist in largely continuous forest.

2.4.4. Maximising the ability to discriminate between correlated models

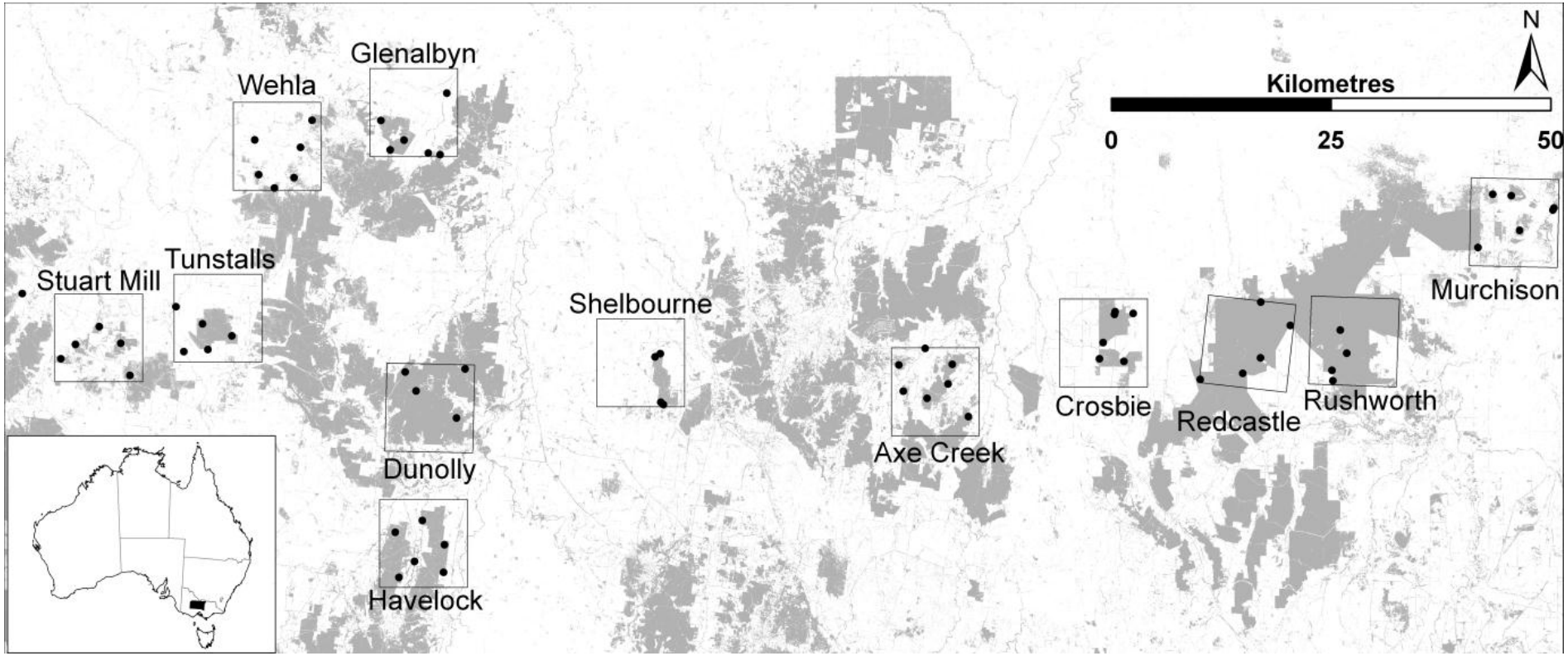
It might be expected that IBR will accumulate over distance, resulting in stronger signals over greater distances. However, in a fragmented landscape these greater distances also increase the number and importance of alternative routes and the number of and complexity of configuration landscape elements that individuals (or gene flow) encounter. One recent set of simulations has suggested that this additional complexity with distance may obscure effects, and, perhaps counter-intuitively, landscape resistance signals may be more prominent at short distances (Jaquiéry et al. 2011). However, other recent simulations across landscapes of equal size, but varying in complexity and cover, found that the best fit of genetic data and landscape resistance was in landscapes with low but aggregated cover and intermediate connectivity (Graves et. al. unpublished manuscript). The comparison of, and discrimination among, correlated models may result in increased Type I error rates (Balkenhol et al. 2009b). Use of 'two stage causal modelling' (Cushman and Landguth 2010, Wasserman et al. 2010), along with separate testing between landscapes of differing cover and aggregation levels at short distance (within landscapes) and longer distance (across study area), in our subsequent testing of predictions with genetic data may help clarify some of these issues. Ultimately, to distinguish unequivocally among correlated landscape models may require extensive, spatially explicit population genetics and demographic simulations across a range of landscape arrangements and relative resistance values, and the development of more powerful statistical techniques to deal with the necessarily pairwise data of landscape genetics (Balkenhol et al. 2009a, Balkenhol and Landguth 2011, Sunnucks 2011).

We have documented a process for making explicit predictions of expected genetic outcomes for a range of species in a system of conservation concern within and among

landscapes based on available data. The process maximises the inferences that can be made about landscape connectivity effects for the system. Our model study system, widespread and relatively abundant birds, means that we have been able to gather good sample sizes for genetic analyses across multiple species. However, this is countered by their high mobility compared with many other organisms, and the small proportion of the populations that we have been able to sample—a result of sampling of many landscape units. Use of prior prediction ensures that the study tests, and if possible extends, our knowledge of the biological reality of connectivity in the system. If we can detect effects in this system, then the presented approach is very likely to be more effective for less mobile species with smaller population sizes. Ideally we would be able to identify a best model for each species. However, if we are able to identify a group of related models, this is likely to determine the importance of connectivity effects for the less well-connected species. This may be sufficient to develop management recommendations for the system as a whole.

Fuscous Honeyeaters (*Lichenostomus.fuscus*) and Yellow-tufted Honeyeater (*L. melanops*, right).

Figure 1: The study area in central Victoria, Australia, showing landscapes, sampling sites and remnant tree cover (shaded).



Values for landscape tree cover (%) are:
1. Landscapes with aggregated tree cover; Shelbourne 12%, Glenalbyn 17%,Tunstalls 20%, Crosbie 26% Havelock 45%.
2. Landscapes with dispersed tree cover; Welha 11%, Stuart Mill 19%, Murchison 27%, Axe Creek 35%.
3. Landscapes with continuous tree cover; Redcastle 75%, Dunolly 79%, Rushworth 79%.

Figure 2: Pairwise resistance as a function of distance from the point nearest to the edge of the grid.

Circuitscape isolation-by-resistance calculated over a linear distance in a circular grid of uniform resistance, 1 unit per cell, cell size 1 unit, and grid radius 500 cells. Each curve represents a different pairwise geographic distance. As a pairwise distance increases, so does the distance from the edge of the grid at which an edge effect of increased resistance distance is apparent. Where the edge of the grid represents an artificial barrier the resistance distance will be overestimated.

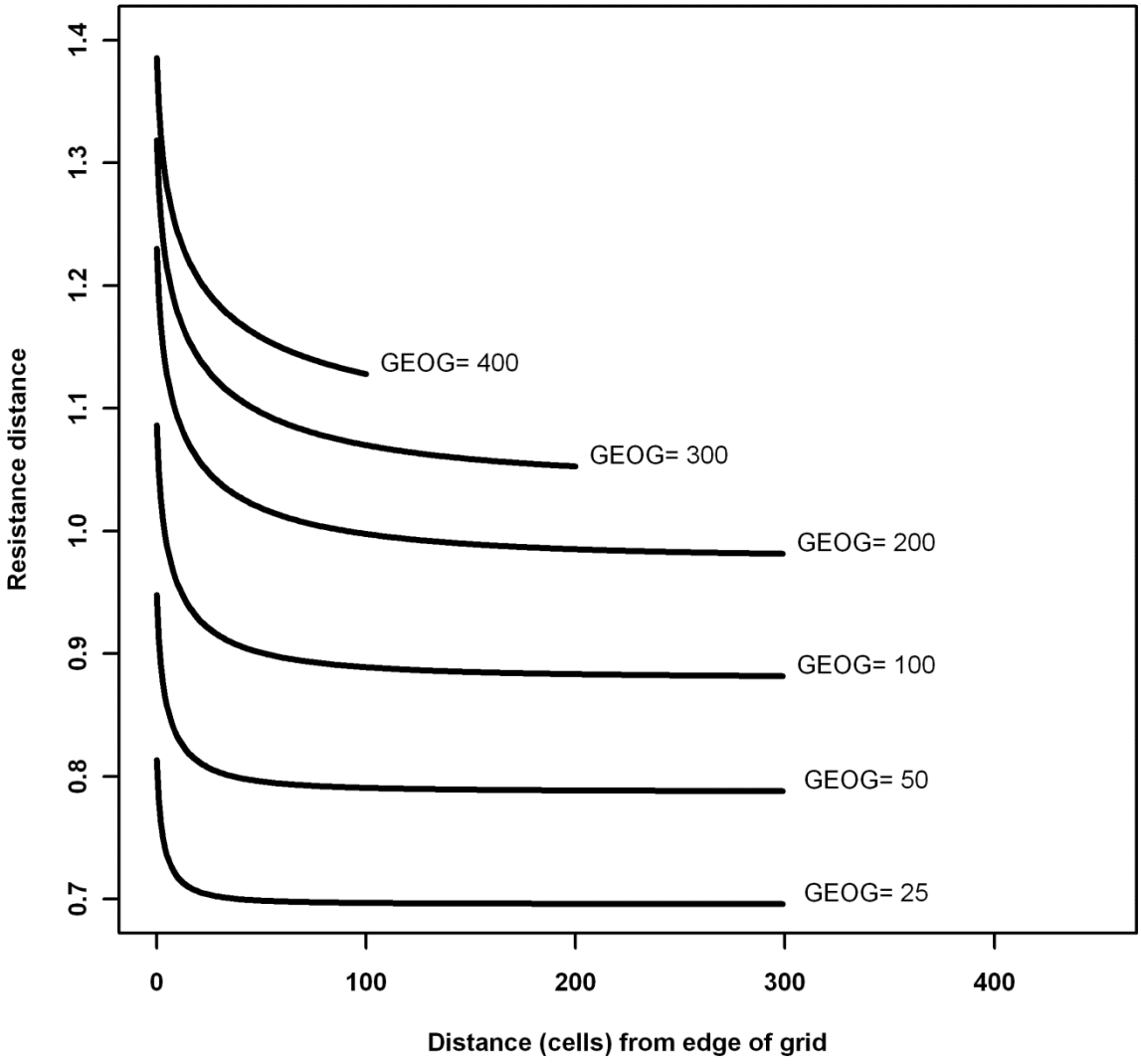


Table 1: Classification of species according to their modelled response to tree cover and their expected mobility.

Mobility	**Response to landscape tree cover**	
	Decliner	**Tolerant**
Mobile	Fuscous Honeyeater (*Lichenostomus fuscus*; FH)	White-plumed Honeyeater (*Lichenostomus penicillatus*; WPH)
Moderate inconclusive[1]	Yellow-tufted Honeyeater (*Lichenostomus melanops*; YTH) Spotted Pardalote (*Pardalotus punctatus*; SPP) Grey Shrike-thrush (*Colluricincla harmonica*: GST) Weebill (*Smicornis brevirostris*; WB)	Striated Pardalote (*Pardalotus striatus*; STP)
Sedentary inconclusive[1]	Eastern Yellow Robin (*Eopsaltria australis*; EYR) Superb Fairy-wren (*Malurus cyaneus*; SFW)	
Sedentary	Brown Treecreeper (*Climacteris picumnus*; BT)	

[1]For mobility, 'inconclusive' is used where there is uncertainty about mobility levels from the literature.

Table 2:Values used for resistance surfaces for developing each landscape model.

Model groups	Resistance surface/model code	Native tree cover	Horticulture/ pine	Unimproved pasture with scattered trees	Crop/improved pasture with scattered trees	Cleared land no scattered trees	Urban	All land cover	Trees	Probable habitat	All other cells
Isolation-by-distance	UNIFORM							1			
Tree cover	TREE_1_2								1		2
	TREE_1_5								1		5
	TREE_1_10								1		10
	TREE_1_100								1		100
Habitat suitability[1]	HAB_1_2									1	2
	HAB_1_10									1	10
Expert Opinion[2]	BT_EO_100	1	2000	1.2	1.2	2000	2000				
	BT_EO_5000	3.07	8000	4000	6000	8000	8000				
	EYR_EO_100	1	1.3	1.3	1.3	2000	2000				
	EYR_EO_5000	2000	6010	6010	8000	10000	10000				
	FH_EO_100	1	1.8	1	1	1	1.8				
	FH_EO_5000	2.17	2010	2010	2010	4010	4010				
	GST_EO_100	1	1.3	1.13	1.3	2000	1.8				
	GST_EO_5000	2.9	2000	7.17	2010	6010	6010				
	SFW_EO_100	1	1.02	2000	2000	2000	1.8				
	SFW_EO_5000	2000	6000	10000	10000	10000	10000				
	WB_EO_100	1	1.8	1.8	1.8	2000	1.3				
	WB_EO_5000	11.6	6010	4000	4000	8000	8000				
	WPH_EO_100	1	1	1	1	1	1				
	WPH_EO_5000	2.62	10.1	5.6	6.32	2010	7.45				
	YTH_EO_100	1	1.8	1	1	1	1.8				
	YTH_EO_5000	2.17	2010	2010	2010	6010	6010				

[1]The habitat suitability models (HAB_1_2 and HAB_1_10) were run separately for each species (because the area and location identified as habitat is different for each species), but are included only once in this table as the same resistance values for habitat and other cells were used for all species.

[2] Species codes for models are given in Table 1. The number at the end of the model code indicates the distance in metres over which resistance was estimated. Estimates for other distances, 200 m, 500 m, 1 km, 2 km and 10 km, which were not used in the final models, are available from the Candidate on request.

Table 3: Variance in expert opinion of land cover resistance to the movement of bird species.

Variance component	All distances	Distance (m)						
		100	200	500	1000	2000	5000	10000
Distance	28							
Expert	7	18	18	22	28	19	8	14
Land cover	9	4	4	5	9	18	21	25
Species	5	3	3	1	1	6	20	14
Residual	51	75	75	72	62	57	50	47

Table 4:Predicted rank of correlation coefficients between landscape models and genetic distances.

Model	Species attributes/requirements for better fit to model	Species									
		BT	**EYR**	**FH**	**GST**	**SFW**	**SPP**	**STP**	**WB**	**WPH**	**YTH**
TREE_1_2	Weak isolation-by-resistance	4=	4=	1=	1=	4=	1=	3=	1=	3=	1=
TREE_1_10	Isolation-by-resistance and strong isolation-by-distance	2=	2=	4=	4=	2=	4=	3=	3=	3=	3=
HAB_1_2	Isolation-by-resistance HAB model provides better identification of suitable dispersal habitat than trees alone	4=	4=	1=	1=	4=	1=	NA	1=	3=	1=
HAB_1_10		2=	2=	4=	4=	2=	4=	NA	3=	3=	3=
EO_5000	Scattered trees important coupled with strong isolation-by-distance	1	1	6	4=	1	NA	NA	3=	3=	3=
No spatial structuring/ panmixia	Highly mobile, 'tolerant'	7	7	3	7	7	6	1=	6	2	6
Isolation-by-distance only rank3		6	6	7	3=	6	3	1=	7	1	7
Isolation-by-distance strength3		Strong	Strong	None	Weak	Strong	Weak	Weak	Weak	Weak	None

1Species codes are given in Table 1.
2For each species, models are ranked from highest (1) to lowest (7).
3The row ranking isolation-by-distance has a rank for the occurrence of isolation-by-distance alone, and strong, weak or none for the strength of the isolation-by-distance signal expected, whether or not isolation-by-resistance is also present.

3. A COMPARISON OF CIRCUIT DISTANCE AND LEAST-COST PATH ALGORITHMS IN A MULTI-SPECIES LANDSCAPE GENETICS ANALYSIS

ABSTRACT

Use of effective distances to simulate the effect of heterogeneous landscapes on individual movements, migration and genetic differentiation between locations in the landscape has become a core technique in landscape genetics. Here I evaluate the two dominant algorithms for summarising effective distances used in modelling complex fragmentation patterns in landscape genetics. Selection of the appropriate null model is important. IBR may be the result of the combination of multiple patch-wise IBD events, where the strength of IBD increases with an increase in landscape resistance. If this is the case, null as well as alternative landscape models should approximate the effects of IBD within homogenous patches of the landscape under consideration. The choice of landscape distance algorithm and null model are important influences on inferences in landscape genetics, and the CS algorithm offers the most suitable general model for the majority of cases for testing of IBR.

3.1. INTRODUCTION

The most widely adopted approaches to estimation of landscape connectivity involve a measure of 'effective distance'; that is, pairwise distance adjusted to reflect interactions between landscape structure and species biology (mobility) that change connectivity, relative to Euclidean geographic distance (Adriaensen et al. 2003). The effective distance can be compared with other estimates of isolation of habitat patches, and tested for correlations with genetic distances among individuals, or populations, of species found in those patches. Two common approaches to modelling of effective landscape distances are LCP distance (Dijkstra 1959, Adriaensen et al. 2003), and the more recent IBR based on CS (McRae 2006). Genetic distances are correlated with a null model of IBD (Wright 1943) and with these effective distances, in a three-stage model selection framework to determine:

- Are genetic differences between populations spatially structured?

- If there is spatial genetic structure, does the incorporation of different effects of landscape elements on gene flow explain genetic distances better than does IBD?
- Which of a set of alternative landscape resistance models best explains the landscape effect?

3.1.1. Least-cost path compared to the circuit distance algorithm

LCP metrics have been criticised as biologically unrealistic because they assume that connectivity equates to the single optimal path between two points, which requires omniscient organisms that unerringly make perfect dispersal decisions. Nevertheless, LCP has been successful in predicting genetic distances in fragmented landscapes (Coulon et al. 2004, Broquet et al. 2006, Epps et al. 2007, Lada et al. 2008b). IBR, through its use of circuit theory and random walk, has a firmer theoretical foundation. IBR provides a more realistic simulation of dispersal and multiple stepwise gene flow processes in heterogeneous landscapes (McRae and Beier 2007, Munshi-South 2012). The number of studies using IBR is growing rapidly (Shirk et al. 2010, Sackett et al. 2012, Walpole et al. 2012, Blair et al. 2013, Trumbo et al. 2013).

Several studies that compare CS and LCP report that CS is a stronger predictor of genetic distances than is LCP. The first published comparisons found that CS explained a greater proportion of genetic differentiation (F_{ST}) across the continental range of two broadly distributed species (Wolverine (*Gulo gulo*) in North America and a Mahogany (*Swietenia macrophylla*) in Central America) than did LCP or IBD modelled as log geographic distance (McRae and Beier 2007). CS also performed better in the case of a contiguous population with interspersed impenetrable matrix for a toad (*Bufo boreas*) bounded by saltwater (Moore et al. 2011). A much smaller scaled study of population connectivity in White-footed Mouse (*Peromyscus leucopus*) in remnant habitat patches of urban New York found CS outperformed LCP in five out of six cases using three estimates of inter-population migration in each of two landscapes (Munshi-South 2012). A study of geckos (*Phyllodactylus tuberculosus*) in fragmented habitat in Mexico found slightly stronger correlations for CS than for LCP, which furthermore included different model parameters (topographic slope was more important in the CS model) (Blair et al. 2013). Two studies have found LCP outperformed CS; that is, provided higher correlations with genetic distances. A study of Wolverines, applying a landscape cover model, found a stronger

correlation of LCP than CS with individual pairwise genetic distance; this was expected because suitable habitat occurred in narrow linear bands along mountain ranges—a scenario in which LCP is expected to outperform CS (McRae and Beier 2007, Schwartz et al. 2009). A study of a dispersal-limited salamander (*Dicamptodon copei*), replicated across three regions of the Pacific north-western USA (Trumbo et al. 2013), found higher correlations of genetic distance with LCP than CS in all three regions, using multiple linear regression on distance matrices (Legendre et al. 1994). In two of the three regions, streams were an important component of the best models—again, linear habitat elements where LCP is expected to perform better than CS.

When comparing the inferences from real spatial genetic data, one cannot be sure which inferences are most accurate because the process(es) that led to the spatial arrangement of genotypes or gene frequencies are not known *a priori*. Spatially explicit simulated genetic data could overcome this problem, since the process that resulted in the spatial arrangement of genotypes and gene frequencies is known. Given that the simulation relies on LCP or CS distance or another algorithm to simulate the effect of heterogeneous landscapes, simulations do not provide unbiased comparisons.

Without a simulation methodology that can reproduce genetic distances across a realistic heterogeneous landscape that is independent of an effective distance algorithm, it is useful to have further empirical comparisons, particularly in multi-species studies that compare results for multiple genetic datasets against the same sets of LCP and CS models. While we cannot know the correct inference in each case, we can use the comparison of the patterns of inferences to better understand the performance of the algorithms.

3.1.2. Choice of appropriate null model and accounting for it with partial correlations

Increasing consideration is being given to the appropriate parameterisation of resistance surfaces that form the basis of models of differential gene flow across heterogeneous landscapes (Spear et al. 2010, Spear et al. 2014). In discussions of the differences between CS and LCP and implications for their use in landscape genetics, the focus has been on identification of patterns of gene flow that one of the algorithms may explain better than the other (McRae and Beier 2007, Schwartz et al. 2009, Spear et al. 2014).

The choice of a null model needed in these comparisons also requires thought and careful justification, but usually is not stated explicitly.

In most studies, Stages 2 and 3 involve partialling out a null model of IBD for testing the fit of observed genetic distance with alternative effective distance models. This removes the effect of geographic distance (i.e. IBD) on genetic distance. However, different null models are not equally successful in meeting this purpose (Amos et al. 2012: Chapter 2 in this thesis).

The model that best approximates the effects of IBD should be used as the null model. However, the effect of IBD on population or individual genetic distances is not well understood. For example, for population-level genetic distance F_{ST}, simulations suggest that under IBD, F_{ST} /1 − F_{ST} (i.e. linearised F_{ST}) is approximately related to log-distance for genetic differentiation in a two dimensional landscape but to linear distance in a one dimensional landscape (Rousset 1997). For individual genetic distances, which are the most useful in looking for landscape effects over short periods of time (Sunnucks 2000), the relationship of genetic distance to geographic distance under IBD is less clear. The relationship with distance may differ from that of population F_{ST}-like measures. Simulations using CDPOP (Landguth and Cushman 2010) found an individual genetic distance—the proportion of shared alleles (Bowcock et al. 1994)—changed non-linearly with distance, reaching an asymptote at relatively short distances. The distance at which the curve plateaued increased with mutation rate and time and the maximum dispersal distance, but was highly variable (Graves 2012).

The most commonly used null models accounting for IBD are Euclidean geographic distance (e.g. Schwartz et al. 2009) and the log of Euclidean geographic distance (e.g. Lada et al. 2008b). Over a uniform resistance surface, the LCP distance is nearly a linear function of distance, and Euclidian geographic distance has, therefore, been used as a null model with LCP. In the analyses below, I use it as the first LCP null model and term the set of models that used the linear geographic distance to approximate IBD LCP&LCP.NULL. I use logarithm ($\log_{10}$) of Euclidean geographic distance as an alternative null model with LCP models and refer to the set of models using this null as LCP&logGEOG.

To assess the contribution of all potential paths in a landscape, CS may be calculated using random walks (McRae 2006). On a uniform surface, the number of paths of similar resistance to the LCP increases rapidly with distance between points, and the rate of increase in CS decreases with this distance. I refer to CSs calculated over uniform surface as CS.NULL. The CS.NULL curve approximates a logarithmic function when calculated for the central zone of a landscape grid but becomes more linear nearer to the edge of the modelled landscape; the area beyond the area of interest is generally set to infinite resistance. Where the edge is an artificial one this aberration can be avoided by including a buffer of landscape equal to the width of the area of interest (Koen et al. 2010, Amos et al. 2012: Chapter 2 in this thesis). However, this CS edge effect may be important in improved modelling of genetic isolation processes. Empirical comparisons suggest CS on a uniform surface (CS.NULL) may provide a better approximation to IBD than either linear or log geographic distance, particularly in bounded and irregularly shaped landscapes (McRae and Beier 2007) and is a better null to compare with CS IBR models. I term the set of models that used CS.NULL as CS&CS.NULL.

In fragmented landscapes, when overall IBR is modelled with discrete resistance values for land cover categories, pairwise effective distances could be considered the combination of IBD processes in each discrete patch of a cover type; a sort of 'patchy IBD' with steeper IBD slopes in the more resistant land cover categories. The algorithm that most effectively models this combined effect of IBD within each patch should provide the best model of IBR, and should be the most successful for identifying an IBR model or for discriminating IBR from IBD. If the selected null model representing IBD on a uniform surface provides a much better model of IBD than the heterogeneous landscape resistance model does of IBR, then IBR could be incorrectly disfavoured. This may be the case for LCP&logGEOG in which the linear nature of the LCP models is a poor analogue for the effects of IBR, if IBR is composed of patch-wise IBD. Where null and IBR use the same algorithm for calculation and both provide good models the resulting inferences should favour neither IBR nor IBD and presumably be the most accurate (i.e. CS&CS.NULL).

As the most appropriate inference based on landscape and genetics data is unknown I make the assumption that it will be approximated by the highest Mantel *r*, particularly for those species predicted to show IBR or IBD (Amos et al. 2012: Chapter 2 in this thesis).

If this is the case, and my interpretation of the behaviour of each of the model sets is correct, then predictions can be made of differences in frequencies of the strongest result, and of the inferences (IBD or IBR) made for all our datasets. One can gain a better understanding of the behaviour of the model sets without concern over the accuracy of any individual result. I predict that for the same genetic distance datasets for the same two dimensional landscape:

- CS and CS.NULL will explain the greater proportion of genetic distance in more cases than will LCP, logGEOG and LCP.NULL; CS being the strongest predictor of IBR or IBD.
- Analysis using CS&CS.NULL will support an inference of IBR more frequently than will LCP&logGEOG; CS being a better model than LCP of IBR.
- Analysis using LCP&LCP.NULL will support an inference of IBR more frequently than will LCP&logGEOG; logGEOG better approximating IBD than does LCP.NULL.
- Analysis using LCP&logGEOG will support an inference of IBD more frequently than will LCP&LCP.NULL or CS&CS.NULL; logGEOG better approximating IBD than does LCP.NULL *and* CS being a better approximation of IBR than LCP.

This paper seeks to test for many species:

- whether a model set comprising CS and CS.NULL is generally a stronger predictor of landscape-related pairwise genetic distances than LCP with a null of either geographic distance or log geographic distance; and
- how different the inferences would be depending on the choice of algorithm and null, and, therefore how important their selection is.

3.2. METHODS

3.2.1. Landscape resistance surfaces and calculation of least-cost path and circuit distance effective distances

In Chapter 2 I presented a series of landscape resistance surfaces to generate pairwise landscape distance hypotheses for 10 woodland-dependent bird species: the White-plumed Honeyeater (*Lichenostomus penicillatus*), Striated Pardalote (*Pardalotus punctatus*), Brown Treecreeper (*Climacteris picumnus*), Eastern Yellow Robin (*Eopsaltria australis*), Fuscous Honeyeater (*L. fuscus*), Grey Shrike-thrush (*Colluricincla*

harmonica), Spotted Pardalote (*Pardalotus punctatus*), Superb Fairy-wren (*Malurus cyaeneus*), Weebill (*Smicronis brevirostris*), and Yellow-tufted Honeyeater (*L. melanops*). Samples for genotyping the birds were collected at 65 locations in a 170 × 50-km area of much-fragmented woodland habitat. The area comprised six land cover classes: native tree cover, horticulture/pine, unimproved pasture with scattered trees, crop/improved pasture with scattered trees, cleared land without scattered trees, and urban areas (Amos et al. 2012, Amos et al. 2014, Chapters 2 and 4 in this thesis).

The landscape resistance surfaces consisted of (a) a set of three general models in which resistance of tree cover to dispersal was set to 1 and resistance of all other land cover classes to 2, 10 or 100 (TREE_1_2, TREE_1_10 and TREE_1_100, respectively), (b) two species-specific models per species based on expert opinion of resistances, for six land cover classes, of a dispersal event of 100 m or 5 km during the lifetime of an individual bird (EO_100, EO_5000, respectively; EO_100 models for the three honeyeaters were indistinguishable from IBD and are not tested here; EO models for the two pardalotes were not built as pardalotes were added to the study after opinions had been elicited), and (c) two models based on a binary species-specific distribution model of habitat *vs*. non-habitat in which the resistance of habitat was set to 1 and resistance of non-habitat was set to 2 or 10 (HAB_1_2 and HAB_1_10, respectively). A null model (of IBD) was created using a surface with uniform resistance with all cells set to a value of 1 (Amos et al. 2012: Chapter 2 in this thesis). I used these resistance surfaces to create two sets of pairwise landscape resistance matrices, CS calculated in Circuitscape 3.5 using focal nodes with eight-cell connection scheme (McRae et al. 2008), and LCP calculated in UNICOR (Landguth et al. 2012a).

From each landscape model and each null model, pairwise effective distances were calculated among all of the 65 sites from which bird genetic samples were collected. Correlations between these pairwise distances for LCP and CS for each resistance surface ranged from 0.12 to 0.96 with a mean of 0.78 (Amos et al. 2012: Chapter 2 in this thesis, Table S3.).

3.2.2. Genetic distances across the same study area for multiple species

Amos et al. (2014: Chapter 4 in this thesis) calculated linearised pairwise F_{ST} (Rousset 1997) and individual genotypic distances (GD, Smouse and Peakall 1999) for each

species and sex among each of the 65 locations. I use those data to compare the results of landscape genetics analyses using the pairwise LCP and CS models described above for the species showing the strongest evidence of spatial genetic structure.

3.2.3. Model testing and selection of the best resistance model

Determining effective dispersal and gene flow in landscapes typically involves pairwise comparisons of highly correlated models, which elevates Type I (false positive) error risk (Cushman and Landguth 2010). I used a modified form of the causal modelling framework (Cushman et al. 2013) that reduces the partial comparisons to the comparison of the best-supported landscape model (the one with the highest significant Mantel *r* value) with the NULL model, to infer IBR, IBD, IBD/R (genetic structure of inconclusive nature) or nil (lack of genetic structure). Full details of the test modifications and interpretation are given in Amos et al. (2014: Chapter 4 in this thesis). I compare the inferences among algorithms and nulls rather than the inferences themselves. Models of gene flow were tested for the eastern and western zones of the study area, for the study area as a whole, and for GD for sexes jointly and separately because of different genetic structures between sexes and in the east and west of our study area (Harrisson et al. 2012, Harrisson et al. 2013, Amos et al. 2014: Chapter 4 in this thesis).

I applied Mantel tests between pairwise linearised F_{ST} or GD for each set of effective pairwise distance models (CS&CS.NULL, LCP&LCP.NULL and LCP&logGEOG) separately. All marginal and partial Mantel tests were performed with 10,000 permutations in R package Ecodist (Goslee and Urban 2007, R Development Core Team 2011).

I compared Mantel *r* values of the marginal Mantel tests across the models to determine whether one algorithm (LCP or CS) explained genetic distances better than the other. The model (CS, LCP, CS.NULL, logGEOG or CS.NULL) with the highest value for marginal Mantel *r* for each species, sex and section of the study area was considered the best-fit model.

3.3. RESULTS

There was little evidence of spatial genetic structure in the study area for six of the 10 species (Harrisson et al. 2012, Harrisson et al. 2013, Amos et al. 2014: Chapter 4 in this

thesis). I restricted my analysis to the four species with clearest evidence of spatial structuring: Brown Treecreeper, Superb Fairy-wren, Eastern Yellow Robin and Yellow-tufted Honeyeater. This resulted in a total of 47 'cases' of genetic distance type, sex, species and area. The sample size was insufficient to test F_{ST} for the Eastern Yellow Robin in the west (Amos et al. 2014: Chapter 4 in this thesis).

3.3.1. Size of Mantel *r* for marginal tests

I found in the study landscapes the CS algorithm explained IBR and IBD better than did LCP and logGEOG respectively in nearly all cases. Prediction 1 (that CS and CS.NULL will explain a greater proportion of genetic variation than will LCP, and LCP.NULL or logGEOG) was supported by the comparison of marginal tests (Table 5 and Table 6); CS provided the highest significant Mantel *r* with GD in 25 of 28 tests and with linearised F_{ST} in 6 of 8 cases. CS or CS.NULL found a significant relationship in seven cases where all of LCP, LCP.NULL and logGEOG were nil. The other 11 cases had nil results with no significant correlation with any of the models.

3.3.2. Comparison of spatial genetic inferences between least-cost path and circuit distance

Comparisons among algorithms were complicated by the many indeterminate inferences; that is, where IBD or IBR were inferred but causal modelling could not discriminate between them. This resulted in potentially consistent inferences between algorithms rather than clear agreement or disagreement.

The choice of algorithm and the null both were important for determining the supported inferences. Agreement of inferences between the three model sets was poor, with only 13–25% of definite agreement and 17–35% clear disagreement in inferences for cases between each pair of model sets (Table 7). In only four cases did three sets of effective distance model agree. When equivocal cases that were caused by the large number of IBD/R results were excluded, there was just 50% agreement in inference between algorithms. There was no clear pattern of differences in the models between inferences based on linearised F_{ST} and GD.

There was some support for Prediction 2, namely, CS&CS.NULL supporting an inference of IBR more frequently than LCP&logGEOG; with 16/35 non-nil cases of CS&CS.NULL and only 8/29 non-nil cases of LCP&logGEOG inferring IBR. Prediction 4

(LCP&logGEOG supporting an inference of IBD more frequently than LCP&LCP.NULL or CS&CS.NULL) was also supported, with 15/29 non-nil inferences of IBD for LCP&logGEOG, compared to 6/35 for CS&CS.NULL and only 1/26 for LCP&LCP.NULL (Table 8). There was little support for Prediction 3 (LCP&LCP.NULL will infer IBR more frequently than will LCP&logGEOG).

Summaries of the causal modelling framework results for LCP&logGEOG and LCP&LCP.NULL are in Appendix D, and for CS+CS.NULL and sample sizes in Amos et al. (2014: Chapter 4 in this thesis, Appendix G tables G1 and G2).

3.4. DISCUSSION

The findings reported here add to the small number of published LCP/CS comparisons indicating that in real landscapes with two dimensional structures, the CS algorithm explains IBR and IBD better than do LCP and log GEOG, respectively (McRae and Beier 2007, Munshi-South 2012, Blair et al. 2013).

The low level of agreement in inferences among the model sets highlights that the choices of landscape distance algorithm and null model, or at least the interpretation of those inferences, are both important decisions in studies making landscape genetics inferences. To determine the circumstances in which each algorithm yields the most accurate inferences of landscape genetics connectivity, one would evaluate genetic datasets where the causal mechanism of the genetic structure was known, not only for a small subsample of locations in the landscape but for all individuals in the landscape. These data cannot be known for real genetic data, and cannot be determined independently of the algorithms in existing spatially explicit landscape genetics simulations. Circularities might be overcome by employing individual-based models using non-grid-based approaches to simulate individual movement through heterogeneous landscapes (e.g. Vuilleumier and Metzger 2006) coupled with individual genotypes over multiple generations in a species for which these processes are well quantified. The number of population genetics simulators, and the range of alternative models upon which they are based, grows (Balkenhol and Landguth 2011, Hoban et al. 2011), and a suitable approach may result from these continuing developments.

Until simulations without circularity are devised we must rely on more empirical studies. The determination of the best model set in this study was limited by the relatively weak correlations between genetic distances and any of the landscape models, and the availability of genetic distance data between a small subset of occupied habitats in the study area due to the limitations of field sampling logistics. A future study using field genetic data would best utilise several species of low mobility where there was a clear *a priori* expectation of strong IBR and IBD.

It seems prudent to use the CS algorithm, which appears to approximate both IBD in uniform landscapes and also IBR in heterogeneous landscapes better than do the alternatives (according to Mantel *r* value), unless there is a strong prior reason for use of an alternative. I have therefore used CS distances in evaluation of the responses to fragmentation in our study system (Amos et al. 2014: Chapter 4 in this thesis).

Table 5: Mantel *r* of significant ($P < 0.05$) marginal tests for each model as a predictor of GD.

The column 'Algorithm with highest Mantel *r*' indicates whether CS,NULL, LCP or logGEOG had the highest value for each sample. The highest value in each row is in bold. Nil results are omitted.

Area	Species	Sex	Predicting algorithm	logGEOG	LCP.NULL	CS.NULL	EO_100	EO_5000	HAB_2	HAB_10	TREE_2	TREE_10	TREE_100	Algorithm with highest Mantel *r*
Study	BT	ALL	LCP	**0.139**	0.128		0.128	0.132	0.129	0.130	0.128	0.131	0.131	CS
			CS			0.142	0.143	0.131	**0.143**	0.138	0.130	0.100	0.084	
		F	LCP	0.127	0.136		0.137	0.151	0.139	0.144	0.140	0.148	**0.151**	CS
			CS			0.134	0.141	**0.179**	0.151	0.169	0.146	0.147	0.143	
		M	LCP	**0.161**	0.131		0.130	0.128	0.130	0.130	0.129	0.129	0.126	CS
			CS			**0.162**	0.157	0.103	0.149	0.125	0.127	0.070	-	
	SFW	ALL	LCP	**0.164**	0.132		0.133	0.130	0.139	0.154	0.136	0.142	0.136	CS
			CS			0.158	0.167	0.132	0.173	0.180	0.196	**0.217**	0.215	
		F	LCP	**0.111**	0.075		0.074	0.090	0.078	0.083	0.077	0.083	0.084	CS
			CS			**0.111**	0.109	0.074	0.090	-	0.095	-	-	
		M	LCP	**0.206**	0.165		0.167	0.156	0.173	0.193	0.169	0.175	0.168	CS
			CS			0.195	0.210	0.170	0.231	0.257	0.265	0.311	**0.317**	
	EYR	ALL	LCP	0.049	0.036		0.037	0.050	0.040	0.046	0.040	0.047	**0.052**	CS
			CS			**0.052**	0.045	-	-	-	-	-	-	
		M	LCP	0.057	-		-	0.061	0.054	0.059	0.054	0.060	**0.065**	LCP
			CS			**0.063**	0.061	-	-	-	-	-	-	
	YTH	ALL	LCP	-		-		-	-	-	-	-	-	CS
			CS			-		-		-	-	0.039	**0.045**	
East	BT	ALL	LCP	**0.130**	0.085		0.084	-	0.082	0.074	0.076	-	-	CS
			CS			**0.147**	0.144	0.092	0.143	0.126	0.126	0.071	-	
		M	LCP	**0.222**	0.146		0.149	0.133	0.149	0.151	0.148	0.122	0.087	CS

Area	Species	Sex	Predicting algorithm	logGEOG	LCP.NULL	CS.NULL	EO_100	EO_5000	HAB_2	HAB_10	TREE_2	TREE_10	TREE_100	Algorithm with highest Mantel *r*
			CS			**0.246**	0.242	0.155	0.236	0.206	0.212	0.119	-	
	SFW	ALL	LCP	0.101	0.108		0.109	0.108	0.111	0.118	0.113	**0.120**	0.116	CS
			CS			0.108	0.116	0.127	0.126	0.147	0.140	0.164	**0.168**	
		F	LCP	**0.091**	0.066		0.067	-	0.067	0.061	0.067	-	-	CS
			CS			**0.105**	0.104	-	0.104	0.095	0.097	-	-	
		M	LCP	0.107	0.146		0.147	0.161	0.150	0.169	0.155	**0.176**	0.173	CS
			CS			0.102	0.118	0.192	0.140	0.194	0.172	0.240	**0.262**	
	YTH	ALL	LCP	**0.037**	-			-	-	-	-	-	-	CS
			CS			**0.049**		-		0.042	0.041	-	-	
		F	LCP	-	-			-	-	-	-	-	-	CS
			CS			**0.095**		-		-	-	-	-	
		M	LCP	-	-			-	-	-	-	-	-	CS
			CS			0.063		0.075		**0.077**	0.067	0.076	-	
West	BT	ALL	LCP	**0.092**	0.073		0.073	0.067	0.071	0.069	0.069	0.060	0.048	CS
			CS			0.097	0.102	0.105	0.109	**0.115**	0.111	0.103	0.094	
		F	LCP	0.054	-		-	**0.087**	-	0.057	0.042	0.067	0.081	CS
			CS			0.062	0.073	**0.157**	0.090	0.136	0.105	0.140	0.148	
		M	LCP	**0.131**	0.117		0.114	0.058	0.106	0.085	0.098	0.060	-	CS
			CS			0.135	**0.135**	0.071	0.135	0.108	0.124	0.077	-	
	SFW	ALL	LCP	**0.256**	0.210		0.209	0.165	0.207	0.205	0.206	0.189	0.148	CS
			CS			0.268	0.273	0.205	0.251	0.190	**0.285**	0.259	0.220	
		F	LCP	**0.217**	0.197		0.194	0.152	0.187	0.159	0.188	0.156	0.105	logGEOG
			CS			**0.212**	0.211	-	0.173	-	0.193	-	-	
		M	LCP	**0.295**	0.222		0.221	0.174	0.222	0.232	0.220	0.213	0.191	CS
			CS			0.323	0.329	0.286	0.314	0.256	**0.352**	0.334	0.302	
	EYR	ALL	LCP	**0.081**	-		-	-	-	-	-	-	-	CS

Area	Species	Sex	Predicting algorithm	logGEOG	LCP.NULL	CS.NULL	EO_100	EO_5000	HAB_2	HAB_10	TREE_2	TREE_10	TREE_100	Algorithm with highest Mantel *r*
			CS			**0.093**	0.068	-	-	-	-	-	-	
		M	LCP	-	-		-	-	-	-	-	-	-	CS
			CS			**0.136**	0.110	-	-	-	-	-	-	
	YTH	ALL	LCP	-	0.019			0.027	0.022	0.025	0.024	0.042	**0.054**	CS
			CS			0.019		-		0.032	0.034	0.053	**0.059**	
		F	LCP	-	0.036			0.045	0.042	0.045	0.046	0.066	**0.078**	LCP
			CS			-		0.046		0.049	**0.050**	-	-	
		M	LCP	0.013	-			0.022	-	-	-	0.033	**0.043**	CS
			CS			0.023		-		0.031	0.035	**0.050**	-	

Table 6: Mantel *r* of significant ($P < 0.05$) marginal tests for each model as a predictor of linearised F_{ST}.

The column 'Algorithm with highest Mantel *r*' indicates whether CS.NULL, LCP or logGEOG had the highest value for each sample. The highest value in each row is in bold. Nil results are omitted.

Area	Species	Predicting algorithm	logGEOG	LCP.NULL	CS.NULL	EO_100	EO_5000	HAB_2	HAB_10	TREE_2	TREE_10	TREE_100	Algorithm with highest Mantel *r*
Study	BT	LCP	0.274	-		0.265	0.270	0.268	**0.280**	0.263	0.273	0.272	LCP
		CS			**0.269**	0.263	0.178	0.260	0.233	0.204	-	-	
	SFW	LCP	0.323	-		0.277	0.228	0.298	**0.338**	0.286	0.292	0.265	CS
		CS			0.275	0.318	0.229	0.420	**0.567**	0.446	0.532	0.542	
	EYR	LCP	-	-		-	-	-	-	-	-	-	CS
		CS			-	0.294	**0.732**	0.370	0.548	0.390	0.568	0.639	
	YTH	LCP	-				-	-	-	-	-	-	CS
		CS			-		-		-	-	0.185	**0.206**	
East	SFW	LCP	-			-	**0.503**	-	-	-	-	-	CS
		CS			-	-	0.528	-	0.494	0.613	0.714	**0.739**	
West	BT	LCP	**0.143**	-		-	-	-	-	-	-	-	logGEOG
		CS			**0.129**	0.119	-	-	-	-	-	-	
	SFW	LCP	0.309	1		0.325	-	0.359	**0.452**	0.354	0.359	-	CS
		CS			0.318	0.372	-	0.481	**0.610**	0.532	-	-	
	YTH	LCP	-	-			-	-	-	-	-	-	CS
		CS			-		-		-	0.230	0.336	**0.340**	

Table 7: Number of agreeing, consistent and disagreeing causal modelling framework inferences between each pair of distance/null algorithms.

Inferences were identified as agreeing for a pair where the same single inference was made for a genetic dataset for both algorithms (i.e. both IBD or both IBR). Where one inference was of IBD/R, and the other IBD/R, IBR or IBD, or they agreed, then the inferences were considered to be consistent with each other. Where one inference was IBD and the other IBR, or where there was an inference using one distance algorithm and a nil result for the other, inferences disagreed. Where both were nil they were not classified.

	CS&CS.NULL / LCP&logGEOG			CS&CS.NULL / LCP&LCP.NULL			LCP&logGEOG / LCP&LCP.NULL		
	F_{ST}	GD	Total	F_{ST}	GD	Total	F_{ST}	GD	Total
Agree	2 (25%)	7 (25%)	9 (25%)	1 (13%)	5 (18%)	6 (17%)	2 (25%)	5 (18%)	7 (19%)
Consistent	5 (63%)	18 (64%)	23 (64%)	4 (50%)	20 (71%)	24 (67%)	4 (50%)	19 (68%)	23 (64%)
Disagree	3 (38%)	10 (36%)	13 (36%)	4 (50%)	8 (29%)	12 (33%)	1 (13%)	5 (18%)	6 (17%)

Table 8: Count of causal modelling framework inferences of each model set for linearised F_{ST}, GD, and total.

	CS&CS.NULL			LCP&LCP.NULL			LCP&logGEOG		
Inference	F_{ST}	GD	Total	F_{ST}	GD	Total	F_{ST}	GD	Total
IBD	1	5	6		1	1	1	14	15
IBD/R	2	11	13	2	12	14	1	5	6
IBR	5	11	16	2	9	11	3	5	8
NIL	3	9	12	7	14	21	6	12	18

DECLARATION FOR THESIS CHAPTER 4

Declaration by candidate

In the case of Chapter 4 the nature and extent of my contribution to the work was the following:

Nature of contribution	**Extent of contribution (%)**
Wrote manuscript, collected genetic samples as principal member of field team, formulated modifications to statistical approach, performed statistical analyses, formulated discussion and conclusions	70

The following co-authors contributed to the work:

Name	Nature of contribution	Extent of contribution (%) (for student co-authors only)
K A. Harrisson,	Contributed to fieldwork, undertook genotyping of samples, discussed findings of papers for which she was principal author (included as appendices to this thesis), commented on manuscript	5
J. Q. Radford	Commented on manuscript, contributed to underlying experimental design, Principal Investigator on funding research grant	
M. White,	Provision of spatial data for model development, comment on manuscript, Partner Investigator on funding research grant	
G. Newell, *	Provision of spatial data for model development, comment on manuscript, Partner Investigator on funding research grant	

R Mac Nally,	Co-supervisor, advice on statistical analysis, comment on manuscript	
P. Sunnucks *	Principal supervisor, detailed comment on manuscript, development of underlying experimental design, Principal Investigator on funding grant	
Alexandra Pavlova	Leader of genotyping laboratory team, contribution of detailed comments and discussion of manuscript and particularly graphical presentation of results	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's signature	[redacted]	**Date** 12/11/2014
Main supervisor's signature	[redacted]	**Date 12/11/2014**

4. SPECIES- AND SEX-SPECIFIC CONNECTIVITY EFFECTS OF HABITAT FRAGMENTATION IN A SUITE OF WOODLAND BIRDS

ABSTRACT

Loss of functional connectivity following habitat loss and fragmentation could drive species declines. A comprehensive understanding of fragmentation effects on functional connectivity of an ecological assemblage requires investigation of multiple species with different mobilities, at different spatial scales, for each sex and in different landscapes. Based on published data on mobility and ecological responses to fragmentation of 10 woodland-dependent birds, and using simulation studies, we predicted that (1) fragmentation would impede dispersal and gene flow of eight 'decliners'—species that disappear from suitable patches when landscape-level tree cover falls below species-specific thresholds—but not of two 'tolerant' species whose occurrence in suitable habitat patches is independent of landscape tree cover; and that fragmentation effects would be stronger (2) in the least mobile species, (3) in the more philopatric sex and (4) in the more fragmented region. We tested these predictions by evaluating spatially explicit IBR models of gene flow in fragmented landscapes across a 50 × 170-km study area in central Victoria, Australia, using individual and population genetic distances. To account for sex-biased dispersal and potential scale- and configuration-specific effects, we fitted models specific to sex and geographic zones. As predicted, four of the least mobile decliners showed evidence of reduced genetic connectivity. The responses were strongly sex specific, but in opposite directions in the two most sedentary species. Both tolerant species and (unexpectedly) four of the more mobile decliners showed no reduction in gene flow. This is unlikely to be due to time lags because more mobile species develop genetic signatures of fragmentation faster than do less mobile species. Weaker genetic effects were observed in the geographic zone with more aggregated vegetation, consistent with gene flow being unimpeded by landscape structure. Our results indicate that for all but the most sedentary species in our system, the movement of the more dispersive sex (females in most cases) maintains overall genetic connectivity across fragmented landscapes in the study area, despite some small-scale effects on the more philopatric sex

for some species. Nevertheless, to improve population viability for the less mobile bird species, structural landscape connectivity must be increased.

4.1. INTRODUCTION

In fragmented landscapes, dispersal and resulting gene flow connect structurally subdivided populations and improve the likelihood of population persistence by increasing probability of recolonising vacant habitat patches, augmenting population sizes and reducing the negative effects of genetic drift and inbreeding (Saccheri et al. 1998, Banks et al. 2007, Fahrig 2007). Thus, an effective conservation strategy would maintain functional connectivity of populations in fragmented landscapes by promoting dispersal and gene flow.

Studying the effects of fragmentation on dispersal and gene flow is challenging because these effects depend on species dispersal abilities, time elapsed since fragmentation, habitat extent and configuration, and spatial scale (Anderson et al. 2010, Landguth et al. 2010b, Short Bull et al. 2011, Sunnucks 2011, Cushman et al. 2013). Sedentary species are usually more affected by fragmentation than are more mobile species (Schmuki et al. 2006, Van Houtan et al. 2007, Shanahan et al. 2010, Callens et al. 2011). Due to sex-specific biases in dispersal, males and females of the same species may respond differently (Stow et al. 2001, Banks et al. 2005, Shanahan et al. 2010). When dispersal is impeded by fragmentation, there may be a deficit of immigrants of the dispersive sex, leading to sex bias towards the philopatric sex in isolated patches (Dale 2001). Altered sex ratios often have negative effects on social structure, demography and microevolution, and, in extreme cases, lead to local extinction (Cooper and Walters 2002). Time lag effects, where the time elapsed since landscape change is insufficient for genetic signatures to have developed may result in failure to detect landscape genetics effects even if gene flow is affected (Landguth et al. 2010b). Presence and detectability of landscape genetics effects also depend on extent and aggregation of habitat and the difference in resistance between ‘habitat’ and ‘non-habitat’, so that different threshold relationships may operate in different landscapes (Cushman et al. 2013). The effects of fragmentation on dispersal also depend on scale: some species show locally constrained dispersal without an apparent pattern emerging at larger scales (Colson et al. 2012), while there may be effects of habitat clearance on long-distance, but not local, dispersal (Blair and Melnick 2012). Even where genetic connectivity occurs through the unconstrained

movement of the dispersing sex at large spatial scales, restricted mobility through fragmented landscapes of the philopatric sex may lead to adverse sex-specific demographic effects at smaller scales (Harrisson et al. 2012, Harrisson et al. 2013). Therefore, a comprehensive understanding of fragmentation effects on functional connectivity of an ecological assemblage requires investigation of multiple species with different mobilities, at different spatial scales, for each sex and in different landscapes.

We applied a multi-species landscape genetics approach (Figure 3) to explore the effects of habitat fragmentation on dispersal and gene flow of an avian assemblage of the Box–Ironbark forests and woodlands of north-central Victoria, Australia (Fig 4A). This region, which had 95% tree cover prior to European settlement in the early nineteenth century, has since suffered extensive vegetation clearing. Substantial clearing began in the 1850s and continued through to the 1940s, with lesser amounts being cleared since; at present, the area has c. 19% of tree cover (DSE 2007, Amos et al. 2012). Many ecological studies in this region have reported continuing decline in woodland-dependent birds over recent decades (Robinson and Traill 1996, Radford and Bennett 2007, Mac Nally et al. 2009). Using data on species occurrence in habitat patches within 10 × 10-km landscapes, Radford and Bennett (2007) showed that these declines are species specific and in many cases depend on the level of tree cover in the 100-km^2 landscapes. The majority of woodland-dependent birds are 'decliners'—species that disappear from apparently suitable patches when landscape-level tree cover falls below species-specific thresholds (Amos et al. 2012). Other species are tolerant of vegetation loss because their occurrence appears to be independent of landscape-level tree cover (Figure 3A).

We hypothesised that reduced dispersal in response to habitat fragmentation underlies the responses of decliners, since the birds are less able or less willing to cross larger gaps separating habitat patches (Robertson and Radford 2009) and because dispersal of tolerant species is unaffected by fragmentation. To test this, we designed a landscape genetics study comparing genetic responses of eight decliners (Brown Treecreeper *Climacteris picumnus*, Eastern Yellow Robin *Eopsaltria australis*, Fuscous Honeyeater *Lichenostomus fuscus*, Grey Shrike-thrush *Colluricincla harmonica*, Spotted Pardalote *Pardalotus punctatus*, Superb Fairy-wren *Malurus cyaeneus*, Weebill *Smicronis brevirostris* and Yellow-tufted Honeyeater *L. melanops*) to those of two tolerant species (Striated Pardalote *Pardalotus striatus* and White-plumed Honeyeater *Lichenostomus*

penicillatus; Figure 3B) (Radford and Bennett 2007, Amos et al. 2012). By using expert opinion and available biological data on birds' mobility, Amos et al. (2012) built general and species-specific spatially explicit models of gene flow across the study region of remnant patches of forest and woodland embedded in largely cleared agricultural land (Figure 3D). These models included IBD (genetic distances increase in proportion to geographic distances) and a set of IBR models that assumed increased levels of resistance to dispersal across cleared land compared to tree cover or modelled habitat.

Here, we tested selected IBD and IBR models (see Landscape Resistance Models below) using individual (genotypic) and population (allele frequencies) genetic distances (Figure 3F). We predicted genetic responses to fragmentation for our 10 target species based on existing knowledge of species mobility (Figure 3C): we expected decliners to show reduced dispersal and gene flow (IBR), with effects more pronounced in less mobile species (Brown Treecreeper, Superb Fairy-wren, Eastern Yellow Robin). For tolerant species, we expected genetic distances either to be spatially unstructured or to increase in proportion to geographic distances (IBD) unaffected by habitat fragmentation (Fig. 1C; Amos et al. 2012). We also expected more pronounced genetic responses to fragmentation for the more philopatric sex: males in all species (Mulder 1995, Doerr et al. 2011, Debus and Ford 2012, Harrisson et al. 2013) except the Grey Shrike-thrush, which has been inferred to have male-biased dispersal (Pavlova et al. 2012) and the Spotted and Striated Pardalotes, for which there was no evidence of sex-biased dispersal (Harrisson et al. 2012). Sex-biased effects of fragmentation were expected to be particularly marked in the obligate cooperative breeders among the target species, the Superb Fairy-wren and Brown Treecreeper—in which male offspring often stay as helpers at the nest—and to some degree in the facultative cooperative breeder, the Eastern Yellow Robin.

We tested models at two spatial scales (whole study area, and east and west zones) because (1) testing for fragmentation effects at different spatial scales can reveal scale-specific effects (Balkenhol et al. 2009a, Segelbacher et al. 2010); (2) broad east–west population structure across the study region was detected by genotype clustering for the Superb Fairy-wren (Harrisson et al. 2013) and Brown Treecreeper (Appendix E); and (3) habitat configuration differed between zones: tree cover was more aggregated in the east than west (Appendix F). Highly aggregated habitat may affect the detectability of landscape genetics responses (Cushman et al. 2011, Short Bull et al. 2011, Cushman et al.

2013), so we might expect stronger responses in the more fragmented western zone than in the eastern zone.

In summary, we investigated species-, sex-, scale- and zone-specific landscape genetics effects on woodland-dependent birds by testing four specific predictions: (1) fragmentation would impede dispersal and gene flow of eight decliners but not of two tolerant species; fragmentation effects would be stronger in the (2) less mobile species, (3) more philopatric sex and (4) more fragmented western zone.

4.2. METHODS

4.2.1. Landscape-resistance models

Using Circuitscape 3.5 (McRae et al. 2008), which integrates the effective distance between points through all possible paths using circuit theory, we built a series of landscape resistance surfaces (Figure 3 D) representing IBR models of gene flow across the study area (Amos et al. 2012). Three to eight IBR models were generated per species based on 25-m pixel rasters of tree cover (TREE_1_2, TREE_1_10, TREE_1_100), expert opinion on the resistance of land cover classes (EO_100, EO_5000) or a binary classification of a species distribution model (Liu et al. 2012) to represent habitat extent (HAB_1_2, HAB_1_10). These models covered a wide range of plausible models given available spatial data and knowledge of the species' responses, and ranged between 1:2 and 1:10,000 in the contrast between areas classed as habitat and the most resistant class of non-habitat, depending on species and model (Appendix G). A null model of IBD was built in Circuitscape using a surface with uniform resistance (Amos et al. 2012). From each IBD or IBR model, pairwise resistance distance matrices among all sites were calculated (Figure 3D).

4.2.2. Sampling

We sampled birds at 63 sites distributed in 12, 10 × 10-km landscapes (from four to seven sites per landscape; Figure 4) chosen to represent a range of tree cover from 11–78% (Amos et al. 2012) in the 50 × 170-km region of Box–Ironbark forests of central Victoria, Australia, building on the design of Radford et al. (2005). Such a study design, which involves local clustered sampling separated by long distances, leads to reduced effective sample sizes because all individuals in local cluster samples have similar cost distances

and geographical distances to other clusters. Reduced sample sizes make the resolution among alternative landscape resistance models difficult (Oyler-McCance et al. 2012), but a clustered design remains the only feasible one for intensively sampling woodland birds using mist nets. We captured and banded birds of the 10 target species (Figure 3B) and collected a small blood sample from each (for genetic analyses) before individuals were released (Amos et al. 2013).

4.2.3. Sexing, genotyping and calculation of genetic distance

Birds were sexed molecularly and genotyped for 6–16 polymorphic nuclear loci (conforming to codominant, autosomal Mendelian expectations, with a mean of 9.7 (s.d. = 8.0) alleles per locus) (Amos et al. 2013, Fig. 1E). Here, we focussed on the effect of fragmentation on dispersal, so we analysed only adults (juvenile and immature birds are not expected to have yet dispersed). For cooperative breeders, some mature offspring remain as 'helpers at the nest' (Noske 1991, Mulder et al. 1994), so probable parent–offspring pairs within sites were identified using parentage analysis in CERVUS 3.0 (Kalinowski et al. 2007) and putative offspring excluded from analyses (for details of Superb Fairy-wren analysis, see Harrisson et al. 2013; for Brown Treecreeper, see Appendix D).

As individual genetic distances are sensitive to missing values, only individuals genotyped at all loci were included in analyses (N = 2198 individuals with N = 53–474 per species; Appendix I). Individual genotypic distances for each pair of adult birds (GD, Smouse and Peakall 1999) were calculated for each species in Genalex 6.41 (Peakall and Smouse 2006). Pairwise F_{ST} values for each pair of site-based samples (where $N \geq 5$) were calculated in Arlequin 3.5 (Excoffier and Lischer 2010). F_{ST} reflects changes in allele frequencies over multiple generations, so it should reflect processes operating on longer timescales than genotype-based GD (Sunnucks 2000). Detection of sex-specific dispersal from non-sex-linked markers relies on distributions of genotypes, not allele frequencies, so we assessed sex-specific differences (see below) using GD but not F_{ST} (Banks and Peakall 2012).

4.2.4. Model testing and resistance model selection

We tested all IBR and IBD models using Mantel and partial Mantel correlations between pairwise resistances and F_{ST} or GD. Determining landscape genetics effects typically involves pairwise comparisons of highly correlated models, elevating Type I error rates (Cushman and Landguth 2010). Despite recent criticisms (Legendre and Fortin 2010, Graves et al. 2013), Mantel and partial Mantel tests, used with care, currently remain the only useable method for these analyses on microsatellite data (Cushman et al. 2013). All tests were performed with 10,000 permutations in the R package Ecodist, version 1.2.7 (Goslee and Urban 2007, R Development Core Team 2011).

Models of gene flow were tested for sexes together and separately. The significant IBR model with the highest marginal Mantel *r* was considered to be the best of a plausible set of IBR models. Where IBD and IBR models were significant ($P < 0.05$), we used partial Mantel tests in a causal modelling framework (Cushman et al. 2013) to determine whether IBR explained the observed genetic structure better than did geographic distance alone. Where both marginal tests but neither partial Mantel test was significant, we concluded that spatial genetic isolation was present but that its nature (IBD or IBR) was indeterminate (denoted IBD/R). To control for the effect of sample size on detectability of sex-specific or zone-specific effects in cases where IBD or IBR was supported in only one sex or zone, we compared Mantel *r* for the best-supported model with bootstrapped 95% confidence intervals of the Mantel *r* in the sex where a landscape effect was not detected. A sex-specific effect was inferred only when the significant Mantel *r* in the supported sex was greater than the upper 95% confidence limit for any resistance model for the unsupported sex.

4.3. RESULTS

4.3.1. The best study area landscape genetics models

Across the whole study area, each type of landscape model (IBD, tree cover-, habitat suitability- and expert opinion-based IBRs) was supported as the model best explaining realised mobility and gene flow for at least one species (Table 9, Appendix J, Appendix K). IBD was the best-supported model for the Grey Shrike-thrush (GD both sexes and males only) and Brown Treecreeper (GD males). Binary tree cover models assuming

higher resistance of treeless than treed areas were the best models of functional connectivity for the less mobile Superb Fairy-wren (TREE_1_10, GD both sexes; TREE_1_100, males only) and for the more mobile Yellow-tufted Honeyeater (TREE_1_100, F_{ST} and GD both sexes). The species-specific habitat distribution model SFW_HAB_1_10 was the best-supported model to explain F_{ST} for the Superb Fairy-wren. Two species-specific expert opinion models that assumed variable resistances of six land cover classes to the probability of a bird dispersing 5 km during its lifetime (EYR_EO_5000 and BT_EO_5000) were deemed to be best for the Eastern Yellow Robin (F_{ST}) and for female Brown Treecreepers.

In some instances, the strongest IBR could not be distinguished from IBD by the causal modelling framework (Cushman, et.al 2013, Appendix K). In each of these cases, IBR was either HAB_1_2 or EO_100 models, which had lowest contrasts between resistance values of different land cover types, and were highly correlated with IBD (correlations between IBD and these IBR models had Pearson R^2 = 0.96–0.99; Amos et al 2012). Conversely, all IBR models supported by the causal modelling framework had high contrasts and were not highly correlated with IBD (R^2 = 0.23–0.64) (Amos et al. 2012).

4.3.2. Testing Prediction 1: fragmentation impedes dispersal and gene flow of eight decliners, but not of two tolerant species

Our prediction that decliners would show landscape genetics signatures of IBR, whereas tolerant species would show either IBD or no genetic structure across the study area (Figure 3C) was supported for nine of 17 tests of the prediction (Figure 3G; Table 1**;** Appendix K). Consistent with predicted responses, IBR was evident for the decliner species the Eastern Yellow Robin (F_{ST}), Superb Fairy-wren and Yellow-tufted Honeyeater (F_{ST} and GD for both), while the tolerant Striated Pardalote and White-plumed Honeyeater exhibited little or no landscape genetics structure with either F_{ST} or GD (Figure 3G). Results were inconclusive for the Brown Treecreeper and Eastern Yellow Robin, as both IBD and IBR were supported by marginal but not partial Mantel tests (Appendix K). Several results ran counter to our projections: there was no landscape genetics structure for the Fuscous Honeyeater (F_{ST} and GD), Spotted Pardalote and Weebill (GD), and there was no support for fragmentation effects on the Grey Shrike-thrush (IBD by GD) (Figure 3G).

4.3.3. Testing Prediction 2: fragmentation effects are stronger in less mobile species

This prediction was partially supported by our results (Table 5; Figure 3G**;** Appendix K). The less mobile decliners (Eastern Yellow Robin and Superb Fairy-wren) exhibited IBR, but genetic structure was independent of landscape resistances for the more mobile decliners (Fuscous Honeyeater, Spotted Pardalote and Weebill) and the more mobile tolerant species (Striated Pardalote and White-plumed Honeyeater; Table 1). Landscape genetics responses for the less mobile Brown Treecreeper and Eastern Yellow Robin were inconclusive. Contrary to Prediction 2, IBR was also supported for Yellow-tufted Honeyeater, one of the more mobile decliners.

4.3.4. Testing Prediction 3: fragmentation effects are stronger in the more philopatric sex

Contrasting male and female landscape genetics responses at the study-wide scale were detected for two species (Figure 3H; Table 5; Appendix K) and sex-specific differences were likely for two more species (Fig. 1H; also Harrisson et al. 2012, Pavlova et al. 2012). The prediction was supported by sex-specific responses for three species. For the Eastern Yellow Robin, genotypic structuring was apparent (although inconclusively IBD or IBR) for the more philopatric males but not for the more dispersive females; for the Superb Fairy-wren, the relatively philopatric males were affected by fragmentation (IBR) but the outcome for females was inconclusive (IBD/R); for the Grey Shrike-thrush, the relatively philopatric females were structured either by IBD or IBR and the more dispersive males showed IBD. The Brown Treecreeper exhibited patterns contrary to the prediction: philopatric males showed IBD but the more dispersive females were strongly affected by fragmentation (IBR). Genotypic distances for both sexes of the Fuscous Honeyeater, Weebill and Yellow-tufted Honeyeater were independent of both geographic distance and landscape resistance.

4.3.5. Testing Prediction 4: landscape genetics effects are stronger in the more fragmented western zone

Although the western and eastern zones of the study region had similar tree cover (30% and 37%, respectively), habitat patches were less aggregated in the west than in the east

(Appendix F); therefore, more instances of IBR were expected in the west. Two species supported this expectation (Table 1; Figure 4B; Appendix K). In the Brown Treecreeper, GD-based IBR was apparent in the west but inconclusive in the east, while F_{ST} tests suggested IBD in the west but no structure in the east. For the Yellow-tufted Honeyeater, there was F_{ST} -based IBR in the west and no structure in the east, and GD-based IBR in the west but inconclusive IBD/R in the east. Greater gene flow and mobility in the east (no genetic structuring) than in the west (IBD) was also evident for the White-plumed Honeyeater and Eastern Yellow Robin (Figure 4B).

4.3.6. Sex-by-zone-specific landscape genetics effects

Sex-specific landscape genetics effects were expected to be more pronounced in the more fragmented western zone. When GDs of sexes were examined separately in each zone, stronger sex-specific responses to fragmentation in the more fragmented west were apparent for three species (Figure 4C, D; Table 5; Appendix K). For the Brown Treecreeper, males in the west showed IBD/IBR and females IBR; whereas males in the east showed IBD and females were unstructured. For the Eastern Yellow Robin, males in the west showed IBD/IBR and females were unstructured, whereas in the east there was no effect in either sex. For the Yellow-tufted Honeyeater, males in the west showed IBD/IBR and females IBR, whereas males in the east showed IBD/R and females, IBD.

4.4. DISCUSSION

4.4.1.1. Reduced dispersal due to fragmentation can explain some but not all patterns of bird disappearance from low tree cover landscapes

Habitat fragmentation appears to reduce dispersal and gene flow for four (of eight) tested decliners, suggesting that some patterns of demographic declines and local extirpations from low tree cover landscapes (Radford and Bennett 2007) can be explained by dispersing individuals avoiding cleared agricultural areas (the poor dispersal 'twinkling lights' extinction mechanism of Ford 2011b). Whereas the Superb Fairy-wren, Eastern Yellow Robin and Yellow-tufted Honeyeater showed evidence of IBR effects when tested for both sexes, results of these tests for the Brown Treecreeper were inconclusive, apparently because the test 'averaged' the effects of contrasting responses of males and females. Testing the sexes separately demonstrated that dispersal of female (but not male) Brown Treecreepers was strongly affected by fragmentation, emphasising the importance of accounting for sex-biased responses in conservation planning. The apparent paradox that the more philopatric sex is less affected may arise if the extreme low mobility of males, less than the width of a few territories (Cooper and Walters 2002, Doerr et al. 2011)**,** means that males fail to encounter non-habitat in heavily cleared landscapes, but females are sufficiently mobile to experience the resistance of unfavourable habitat. Similarly, simulations by (Landguth et al. 2010a) showed that more mobile species exhibit genetic structuring resulting from effects of novel barriers to dispersal in fewer generations than do less mobile species. However, isolation effects will depend on the scale of mobility relative to the grain of habitat distribution, so such effects can differ among circumstances and types of organism (e.g. sexes and species).

In the four remaining decliners, unlike the cases just discussed, reduced gene flow and genetic connectivity could not explain their loss from low-cover landscapes. An alternative explanation, namely, that the time since landscape alteration was insufficient for development of a genetic signal, in these species appears unlikely given that we detected IBR for the most sedentary species in our system and that mobile species develop signs of a barrier to gene flow faster than do sedentary species (Landguth et al. 2010b). Given that gene flow in these four declining species appears to be unaffected by loss of structural connectivity, other processes not tested here must be responsible for

population declines in fragmented landscapes, notably low resource availability in landscapes with low tree cover ('turning down the dimmer switch' extinction mechanism of Ford 2011a), and other biological impacts such as disturbed mating systems and disruption of cultural connectivity (Pavlova et al. 2012, Harrisson et al. 2013).

4.4.1.2. Less mobile species tend to suffer more from fragmentation than do more mobile species

Despite considerable differences among species in response to loss of structural connectivity, mobility appears to be an important predictor of landscape effects on genetic differentiation. Sedentary species appear more sensitive to fragmentation than are more mobile ones. Among the four species displaying reduced dispersal as a response to fragmentation, the Brown Treecreeper, Eastern Yellow Robin and Superb Fairy-wren are the most sedentary species we studied and Yellow-tufted Honeyeater is the least mobile of the three honeyeater species. Apart from the Grey Shrike-thrush, the other decliners that showed little genetic response to fragmentation are relatively mobile, and the two species tolerant to fragmentation are mobile (Higgins et al. 2001, Higgins and Peter 2002, Higgins et al. 2006). Finding support for IBR for the relatively mobile Yellow-tufted Honeyeater but not for the less mobile Grey Shrike-thrush, Spotted Pardalote and Weebill might be in part due to sample size (Appendix I).

4.4.1.3. Fragmentation can affect both the philopatric and dispersive sex

Tests for sex-specific effects of fragmentation over the whole study area and in the more fragmented western and more aggregated eastern zones showed potential sex biases in landscape genetics responses for seven species. However, only for the Brown Treecreeper and Superb Fairy-wren could stronger effects of fragmentation (IBR) be conclusively inferred for only one sex. Males in both species are philopatric, but in the Superb Fairy-wren, philopatric males were seemingly more affected by fragmentation than were the females (males showed IBR, whereas IBD could not be rejected in favour of IBR for the more dispersive females), whereas in the Brown Treecreeper, the dispersive females showed IBR due to habitat fragmentation in the whole study area and the west but the philopatric males showed only IBD in the whole study area and the east, and IBD/R in the west. It is possible, and consistent with the extreme philopatry seen in male Brown Treecreepers (Cooper and Walters 2002, Doerr et al. 2011), that pervasive natural IBD in males masks IBR caused by landscape change. By this argument, male Superb Fairy-

wrens, although the more philopatric sex of their species, must be sufficiently mobile to experience fragmentation.

Different effects of fragmentation on the dispersal of the two sexes may lead to fragmentation-associated disruption to the complex breeding systems and inbreeding avoidance mechanisms of the Brown Treecreeper and Superb Fairy-wren (e.g. increased levels of inbreeding in philopatric males, reduced immigration of females and novel genes). This may leave small, isolated populations more vulnerable to local extinction (Blackmore et al. 2011, Harrisson et al. 2013). Evidence of such an effect is most apparent in the Brown Treecreeper, where the restriction of female dispersal (IBR) in fragmented but not in contiguous vegetation, coupled with strong male philopatry (IBD) in contiguous and fragmented habitat, supports earlier findings that decreased immigration of females into isolated patches is a primary cause of local extirpation in this species (Cooper and Walters 2002, Cooper et al. 2002).

Consistent with the general pattern of greater philopatry in male passerines and the expectation of stronger spatial structure in the more philopatric sex, IBD or IBD/R was found for males with no corresponding genetic structure in females for three species: the Brown Treecreeper in the eastern zone, Eastern Yellow Robin in the study area and in the west and Striated Pardalote in the east. There were no counter examples of female-specific genetic structuring. For the Grey Shrike-thrush, fragmentation effects on philopatric females were inconclusive (IBD/R), whereas males showed structure consistent with IBD: lack of resolution, as well as lack of structure on smaller spatial scales, could be due to small sample sizes for this species.

4.4.1.4. Fragmentation effects are more pronounced in the geographic zone where habitat patches were more dispersed

Stronger landscape genetics responses to fragmentation in the west and greater gene flow and dispersal in the east detected for three species could be related to the higher level of vegetation fragmentation in the west. The simulations of Cushman et al. (2013) showed that genetic structure will be significantly related to landscape structure (independent of Euclidean distance) only when habitat is highly fragmented, and they warned that in many real landscapes where habitat is aggregated it may not be possible to identify IBR, even if it is actually shaping genetic distances. Therefore, it appears that splitting the

analyses into zones with different levels of vegetation aggregation gives additional power to detect IBR, given sufficient sample sizes.

4.4.1.5. Observed isolation effects were weaker than predicted, although still detectable for the species most expected to show effects

Effects of reduced connectivity following habitat fragmentation may be expected to be weaker in birds, with their higher vagility, than in flightless terrestrial vertebrates (With et al. 1997). However, many species of birds, including those described here, have behavioural constraints to crossing even small (hundreds of metres) gaps, in at least some circumstances (Bosschieter and Goedhart 2005, Doerr et al. 2011). Short-distance, frequent movement decisions do not necessarily translate into longer distance dispersal, in part because rare long-distance dispersal events are difficult to detect even with intensive observations (Morales and Ellner 2002). Failure to detect rare long-distance dispersal events leads to the underestimation of dispersal ability and functional connectivity. There is recent evidence that dispersal and gene flow of woodland-dependent bird species may greatly exceed observed dispersal distances even in an extremely philopatric species in fragmented habitat (Blackmore et al. 2011). The failure to detect isolation effects for the Spotted Pardalote, Striated Pardalote, Weebill and Fuscous Honeyeater suggests substantial mobility and gene flow in these species. It is unlikely that the time since landscape alteration was insufficient for development of a genetic signal of IBR, given the signal found in the more sedentary species (see above).

Notwithstanding the potential for undetected dispersal by birds in large areas of vegetation, we found strong evidence that fragmentation of tree cover reduced individual dispersal in at least three decliner species (Brown Treecreeper, Superb Fairy-wren and Yellow-tufted Honeyeater). In addition evidence that fragmentation of tree cover reduced gene flow was found in the Eastern Yellow Robin. The estimates of degree of resistance of ‘non-habitat’ components in the best models of IBR were at least as great as those reported for two resident, sedentary forest-dependent passerines in eastern Australia (White-browed Scrubwren,*Sericornis frontalis* and Yellow-throated Scrubwren, *Sericornis citreogularis*), and comparable to those in a resident passerine in North America (Song Sparrow (*Melospiza melodia*)) (Shanahan et al. 2010, Unfried et.al 2012). However, all cases with equal support for IBD and IBR models had IBR models with relatively low resistance of ‘non-habitat’, making the two difficult to distinguish.

The use of multiple landscapes, scales of analysis and landscape configurations allowed us to identify landscape genetics patterns that may have been overlooked in a single-study area approach, and also some thresholds of landscape configuration that may otherwise have obscured real effects (Cushman et al. 2011, Short Bull et al. 2011). This was enhanced by our capacity to compare and contrast the response of a diversity of species in those landscapes. Our approach necessarily resulted in some compromises. The power of this study to detect isolation effects in some species, particularly at the east and west zones scale, was limited by sample size or the number of genetic loci available for each species. Limited number of markers and relatively low variation within markers reduced power to discriminate a landscape model (IBD or IBR) and contributed to a failure to distinguish among competing IBD/IBR models(Cushman et al. 2013). Therefore, it is likely that we have underestimated the magnitude of effects of fragmentation in our system. Power is likely to increase more through having more sampled loci per individual than by having more individuals (Landguth et al. 2012b), at least where sampling locations are sufficient to capture the variation in landscape patterns and individual species responses. Multi-species studies such as ours are becoming increasingly feasible with high throughput sequencing and genotyping methods, allowing greater resolution among alternative landscape models (Allendorf et al. 2010). However, large scales and high-intensity capturing of wild birds (or other wildlife) seems set to remain a considerable undertaking without a revolution in capture techniques. Individuals should be sampled from independent locations, but the realities of intensive field sampling usually lead to clustered or nested samples. Emerging more flexible modelling approaches, such as those proposed by Bradburd et al. (2013) using Bayesian estimation of genetic differentiation and spatial structure with landscape attributes, may better account for the sampling structure.

Summary

We sought a broad understanding of the effects of vegetation fragmentation on functional connectivity for an avian assemblage of the Box–Ironbark region of south-eastern Australia. We applied a landscape genetics approach involving multiple species with different mobilities tested at different spatial scales, for each sex and in landscapes with varying habitat aggregation. We demonstrated that (1) reduced functional connectivity (e.g. dispersal leading to gene flow) due to loss of structural connectivity (fragmentation)

can explain observed patterns of bird occurrences for some declining species (other factors such as habitat extent and resource availability or edge effects probably are important for other decliners); (2) habitat fragmentation is a more serious conservation issue for sedentary or low-mobility species, although fragmentation may also impede dispersal of mobile species; (3) responses to fragmentation can be sex specific, so that species mobility and the mobility of each sex need to be considered in conservation planning with both the more philopatric and the more dispersive sexes potentially being affected by fragmentation but due to different mechanisms; and (4) even for landscapes with similar levels of habitat cover, aggregation of habitat is an important determinant of landscape genetics response to fragmentation, with fewer negative effects observed in more aggregated areas. We observed weaker landscape genetics effects than predicted, which may be partially attributable to higher than expected mobility of the birds on the spatial scale of the study area, small sample sizes, clustered study design, low marker variability and low resistance of non-habitat to movement for some species. Reduced functional connectivity appears to be only one of several processes leading to the ongoing decline of birds in this heavily cleared and degraded ecosystem (Ford 2011a). Measures to address declines of the most sedentary species would include improving structural connectivity and retention of scattered trees to assist dispersal through cleared land. For decliner species not strongly affected by limited mobility, improving habitat patch quality and resource extent may be more effective than connecting habitat.

Table 9: Summary of results supporting four specific and two general predictions

See Figure 3 legend for species abbreviations. CMF, tests within causal modelling framework (Appendix K); IBR, isolation-by-resistance model; IBD, isolation-by-distance. Results for between sex or zone comparisons in italics were significant, but were not supported by comparison of bootstrapped confidence intervals for Mantel *r*.

Predictions	Analyses performed to test predictions	Results wholly or partially supporting prediction	Results not supporting prediction
1. Fragmentation should impede dispersal and gene flow of eight decliners (BT, EYR, FH, GST, SPP, SFW, WB, YTH), but not of two tolerant species (STP, WPH)	CMF tests for both sexes across the study area using F_{ST} and GD (Figure 3G)	EYR: IBR (EO_5000) using F_{ST}; SFW: IBR (HAB_1_10) using F_{ST}, IBR (TREE_1_10) using GD; YTH: IBR (TREE_1_100) using F_{ST} and GD; STP: no response using F_{ST} or GD; WPH: no response using F_{ST} or GD	FH: no response using F_{ST} or GD; SPP and WB: no response using GD; GST: IBD (not IBR) using GD; BT: inconclusive IBD/IBR (EO_100) using F_{ST}, inconclusive IBR/IBR (HAB_1_2) using GD; EYR: inconclusive IBD/IBR (EO_100) using GD
2. Fragmentation effects should be stronger in the less mobile species (BT, SFW, EYR)	CMF tests for both sexes across the study area using F_{ST} and GD (Figure 3G)	EYR (less mobile): IBR using F_{ST}; SFW (less mobile): IBR using F_{ST} and GD; FH, STP, WPH (more mobile): no structure using F_{ST} or GD; SPP and WB (more mobile): no structure using GD	YTH (more mobile species, yet least mobile honeyeater): IBR using F_{ST} or GD; BT (less mobile): inconclusive IBD/IBR using F_{ST} or GD; EYR (less mobile): inconclusive IBD/IBR using GD GST (less mobile): IBD (not IBR) using GD
3. Fragmentation effects should be stronger in the more philopatric sex (males in BT, EYR, FH*, SFW, WB, YTH; females in GST). *In (Harrisson et al. 2013) sex-biased	Separate CMF tests for females and males using GD (Figure 3H)	EYR: inconclusive IBD/IBR (EO_100) in philopatric males while no structure in females; GST: inconclusive IBD/IBR (EO_100) for philopatric females while IBD for males; SFW: IBR (TREE_1_100) in	BT: IBD in philopatric males while IBR (EO_5000) in females; FH, WB and YTH: no structure in either sex

Predictions	Analyses performed to test predictions	Results wholly or partially supporting prediction	Results not supporting prediction
dispersal for FH was not statistically significant		philopatric males while inconclusive IBD/IBR (EO_100) in females	
4. Fragmentation effects should be stronger in the more fragmented western zone than in the more aggregated eastern zone	Separate CMF tests for eastern and western zones using GD and F_{ST} (Figure 4B, legend for Figure 4)	BT: IBD in the west while no structure in the east using F_{ST}, IBR (HAB_1_10) in the west while inconclusive IBD/IBR in the east using GD; YTH: IBR (TREE_1_100) in the west while no structure in the east using F_{ST}, IBR (TREE_1_100) in the west while inconclusive IBD/IBR in the east using GD	GST, FH, SPP, WB: no structure in the west or east using GD; FH: no structure in the west or east using F_{ST}; SFW: inconclusive IBD/IBR in the west while IBR in the east using F_{ST}
5. Zone- and sex-specific effects: sex-specific fragmentation effects should be more pronounced in the more fragmented western zone	CMF tests by sex for eastern and western zones using GD (Figure 4C and D)	BT: west—inconclusive IBD/IBR in males, IBR in females; east—IBD in males, no structure in females; EYR: west—IBD/IBR in males, no structure in females; east—no structure in either sex; YTH: west—inconclusive IBD/IBR in males, IBR in females; east-inconclusive IBD/R in males, IBD in females	GST: west and east—no structure for either sex; SFW: west and east—IBR in males, inconclusive IBD/IBR in females; STP: west- no structure in either sex; east—inconclusive IBD/IBR in males, no structure in females

Figure 3: Workflow of the project design and whole of study area result summary

(A) Radford and Bennett (2007) found that some woodland bird species are tolerant to the effect of habitat removal, whereas some disappear from suitable patches in 10 × 10-km landscapes if the amount of tree cover falls below a species-specific threshold level.

(B) Amos et al. (2012) described the study design in which tolerant and decliner species of different mobility are sampled for genetic analyses from 12 of the 10 × 10-km landscapes used by Radford and Bennett (2007). The tolerant species were Striated Pardalote (STP) and White-plumed Honeyeater (WPH), decliners were Brown Treecreeper (BT), Superb Fairy-wren (SFW), Eastern Yellow Robin (EYR), Grey Shrike-thrush (GST), Weebill (WB), Spotted Pardalote (SPP), Yellow-tufted Honeyeater (YTH) and Fuscous Honeyeater (FH).

(C) Based on prior knowledge of mobility and assuming that fragmentation impeded dispersal of decliners, Amos et al. (2012) predicted genetic responses (isolation-by-distance, IBD, isolation-by-resistance, IBR, or none) for the 10 target species.

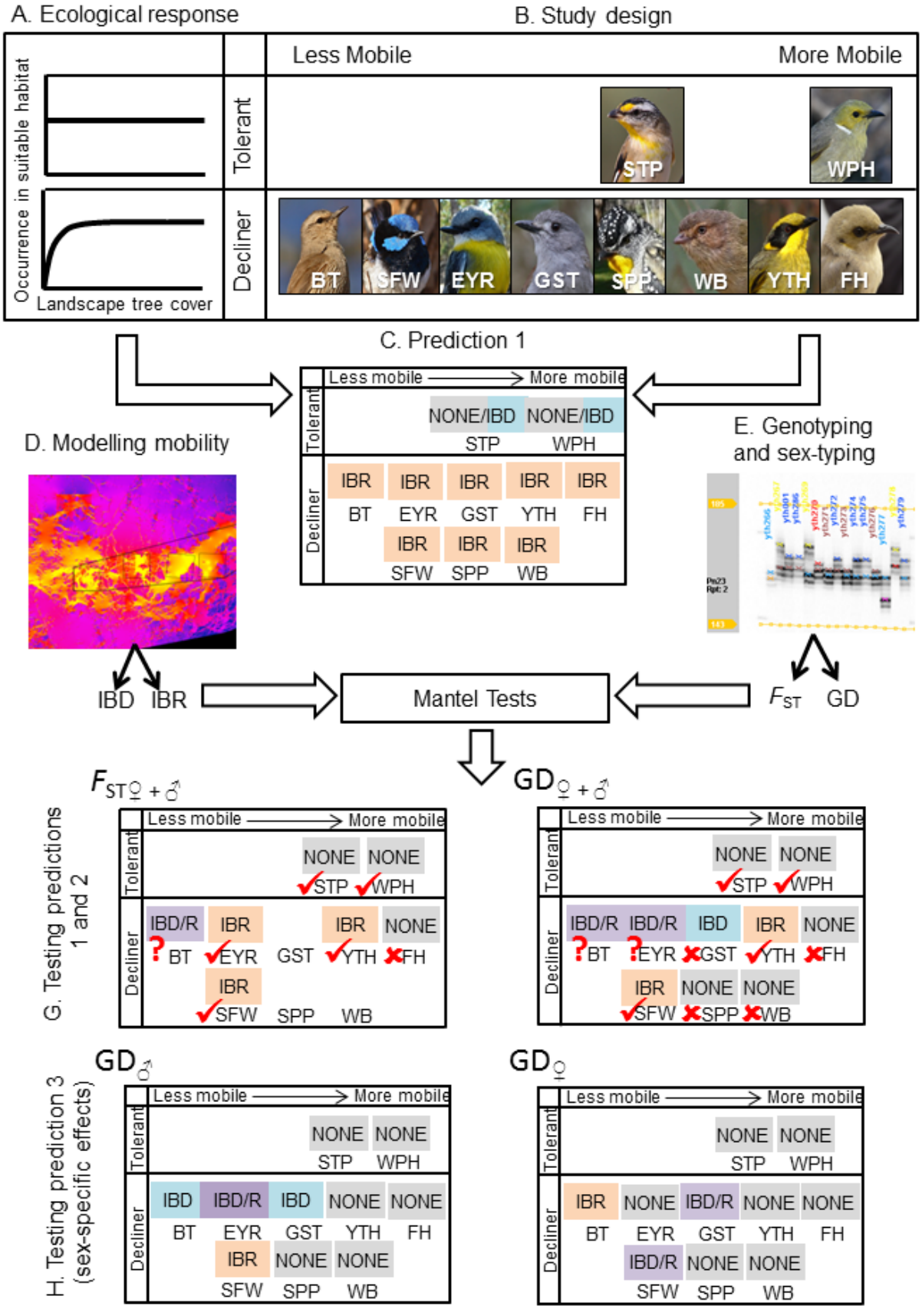
(D) Using expert opinion and available biological data, Amos et al. (2012) built numerous species-specific, spatially explicit prior models of gene flow through fragmented landscapes in Circuitscape. From these models, pairwise per-site landscape resistance distances representing IBD or IBR were calculated (here, different IBR models have been reduced to the single category for simplicity, but see Appendix K).

(E) Birds of each of 10 species were genotyped for microsatellites and other length-variable markers and sexed following Harrisson et al. (2012, 2013, 2013b) and Pavlova et al. (2012, 2013), and genetic distances (pairwise per-individual distances, GD, or per-site population F_{ST}) were calculated.

(F) Mantel tests were used to test whether geographic distances (IBD) or landscape resistances (IBR) explained variance in genetic distances (GD or F_{ST}). If significant associations between landscape and genetic distances were detected, then partial Mantel tests and causal modelling framework were applied to infer whether one or more of the IBR models (i.e. models of gene flow that assume reduced dispersal through fragmented landscapes) explain variance in genetic distances over and above what is explained by geographic distances alone (IBD).

(G) Results of the tests of alternative landscape models denoted by red ticks met the predictions of Amos et al. (2012), whereas those denoted by crosses did not (blank cells for some species indicate that tests were not performed due to small sample sizes). IBD/R denotes cases where IBD and IBR could not be distinguished by causal modelling (see Appendix K for details).

(H) Tests of the models performed on males and females separately showed sex-specific effects of fragmentation for at least two sedentary species with female-biased dispersal: BT and EYR. Fine-scale effects of fragmentation on the other two species potentially showing sex-specific effects, SFW and GST, were described in Harrisson et al. (2013) and Pavlova et al. (2012), respectively.


A. Ecological response
B. Study design
Occurrence in suitable habitat
Landscape tree cover
Tolerant
Decliner
Less Mobile
More Mobile
STP
WPH
BT
SFW
EYR
GST
SPP
WB
YTH
FH
C. Prediction 1
Less mobile
More mobile
NONE/IBD
IBR
D. Modelling mobility
E. Genotyping and sex-typing
IBD
IBR
Mantel Tests
F_{ST}
GD
G. Testing predictions 1 and 2
F_{ST} ♀ + ♂
GD ♀ + ♂
IBD/R
NONE
H. Testing prediction 3 (sex-specific effects)
GD ♂
GD ♀

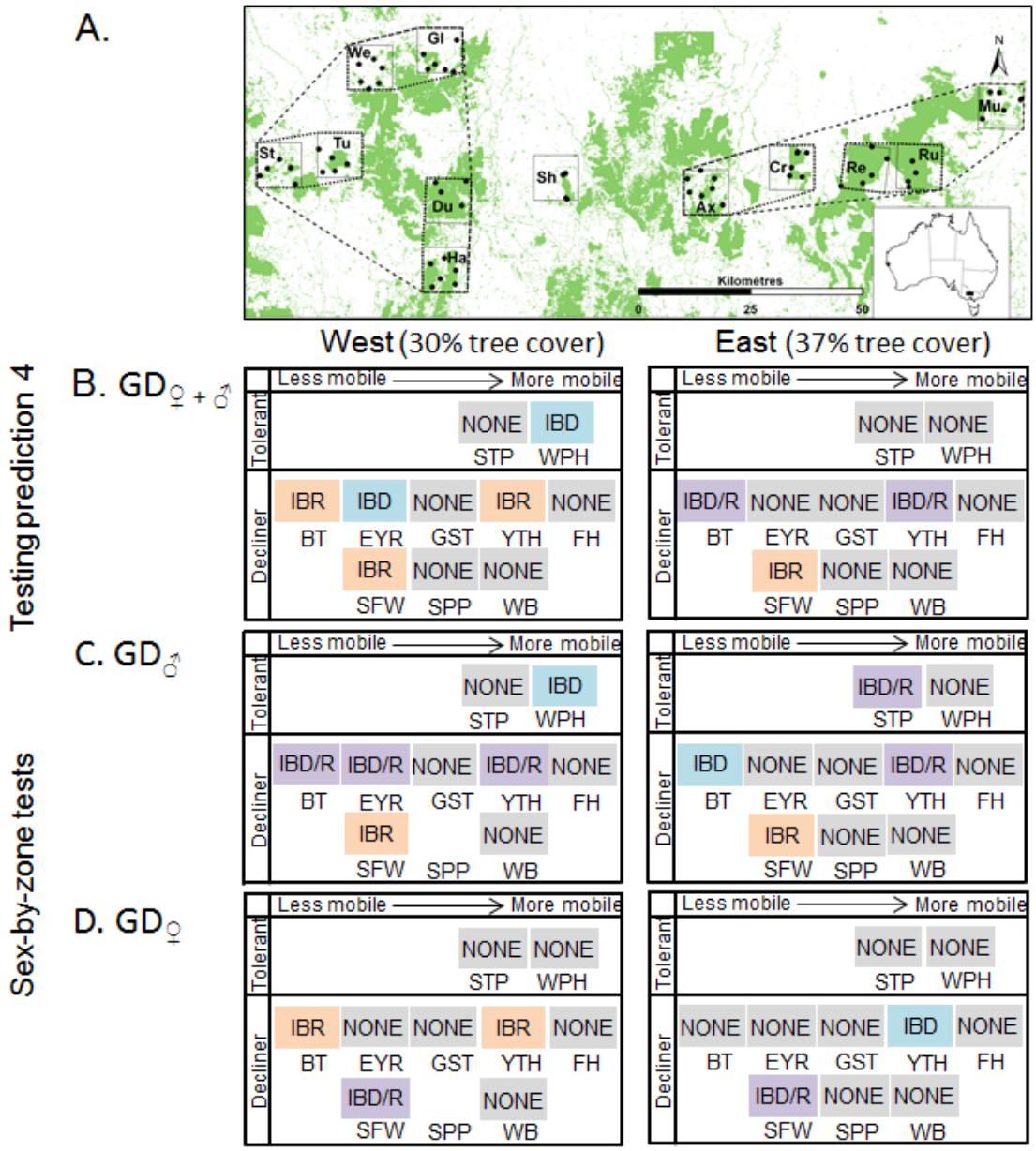


Figure 4:. Zone and sex-by-zone tests

Study area in central Victoria, Australia (A) and tests for scale- and zone-specific effects of fragmentation (B–D) on 10 woodland birds performed on west and east zones (dashed lines on the map) using individual genetic distances (GD) for both sexes (B), males (C) and females (D). The landscape map shows original landscapes (solid lines), sampling sites (dots) and remnant tree cover (shading). Details of the study area and landscape abbreviations are given in Amos et al. (2012). Genetic responses (isolation-by-distance, IBD, isolation-by-resistance, IBR, or none) between west and east zones are compared (IBD/R denotes cases where IBD and IBR could not be distinguished by causal modelling). Species abbreviations are as in the legend for Figure 3.

DECLARATION FOR THESIS CHAPTER 5

Declaration by candidate

In the case of Chapter 5, the nature and extent of my contribution to the work was the following:

Nature of contribution	**Extent of contribution (%)**
Wrote manuscript, collected morphometric and haematological data as principal member of field team, performed genetic and statistical analyses, formulated discussion and conclusions	60

The following co-authors contributed to the work:

Name	**Nature of contribution**	**Extent of contribution (%) for student co-authors only**
S. Balasubramaniam,	Contributed to fieldwork and general discussion of project, briefly commented on manuscript	
L. Grootendorst	Honours student, undertook initial analyses of a subset of these data for four species for her Honours thesis. Briefly commented on manuscript	10
K.A. Harrisson	Contributed to fieldwork, undertook genotyping of samples, commented on manuscript	5
A. Lill *	Initial field team leader, supervisor for L Grootendorst, developed initial haematological study proposal	
R. Mac Nally	Co-supervisor for J.N. Amos, discussion of experimental and statistical approaches, comment on manuscript	
A. Pavlova	Leader of genotyping laboratory team, discussion of experimental approach and advice on genetic analyses. Comment on manuscript	
J.Q. Radford	Involved in initial experimental design as Principal Investigator on grant funding the project. Comment on manuscript	
N.Takeuchi	Field team coordinator, laboratory assistant genotyping samples	
J. R. Thomson	Advice and assistance in development of statistical analyses, commented on manuscript	
P. Sunnucks *	Principal supervisor for J.N. Amos, co-	

	supervisor for L. Grootendorst. Developed initial haematological study proposal. Principal Investigator on grant funding for the project, commented on manuscript	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's signature	[redacted]	**Date** 12/11/2014
Main supervisor's signature	[redacted]	**Date 12/11/2014**

5. LITTLE EVIDENCE THAT CONDITION, STRESS INDICATORS, SEX RATIO OR HOMOZYGOSITY ARE RELATED TO LANDSCAPE OR HABITAT ATTRIBUTES IN DECLINING WOODLAND BIRDS

ABSTRACT

Habitat loss, fragmentation and degradation are drivers of major declines in biodiversity and species extinctions. The actual causes of species population declines following habitat change are more difficult to discern and there is typically high covariation among the measures used to infer the causes of decline. The causes of decline may act directly on individual fitness and survival, or through disruption of population processes. We examined the relationships among configuration, extent and status of native vegetation and three commonly used indicators of individual body condition and chronic stress (haemoglobin level, haematocrit, residual body mass condition index) in 13 species of woodland-dependent birds in south-eastern Australia. We also examined two measures of changes to population processes (sex ratio and individual homozygosity) in 10 species and allelic richness in five species. We found little support for relationships between site or landscape characteristics and individual or population response variables, notwithstanding that our simulations showed we had sufficient power to detect relatively small effects. We discuss possible causes of the absence of detectable habitat effects in this system and the implications for the usefulness of individual body condition and easily measured haematological indices as indicators of the response of avian populations to habitat change.

Key words: Landscape ecology, habitat change, vegetation condition, body condition, residual body mass, haemoglobin, haematocrit, individual homozygosity, allelic richness and sex ratio.

5.1. INTRODUCTION

Habitat loss and fragmentation are well established as the most prevalent causes of anthropogenically induced biodiversity loss through local and global population decline

and extinction (Fahrig 2003, World Resources Institute 2005). However, the identification of the mechanisms of these negative effects has proven more difficult to establish. Species responses to loss and degradation of habitat differ greatly (Mönkkönen and Reunanen 1999, Bennett and Radford 2009) because a wide range of life history traits can be affected by fragmentation (Banks et al. 2007). There is often covariation of many landscape and site attributes (e.g. habitat clearance, fragmentation of remnants and decrease in mean remnant size and remnant structure and condition) that may influence whether an area can support a population (Saunders et al. 1991, Yates and Hobbs 1997, Ewers and Didham 2005, Lindenmayer and Luck 2005 , Radford et al. 2005). Despite this problem, biodiversity protection and restoration require the teasing apart of the processes underlying biodiversity declines that are the consequence of habitat loss, fragmentation and degradation (Lindenmayer and Fischer 2007). There is a considerable tension in the literature between those emphasising the importance of extrinsic and stochastic factors in determining population decline following habitat loss (e.g. Caughley 1994), and those who argue for an important, though often difficult to detect, role for intrinsic factors (such as individual condition and genetics) in population declines (Arcese 2003).Species declines may result directly from loss of habitat or indirectly through changes in population processes due to habitat fragmentation. Vegetation structure is a common determinant of avian diversity and individual species habitat preferences (Rotenberry 1985, Mac Nally 1990). Human-induced changes to vegetation structure decrease habitat suitability for some species while increasing it for others (Lindenmayer et al. 2008). Reduction in the size and increase in edge ratio of patches in fragmented forests and woodlands can lead to decreased vegetation condition (Yates and Hobbs 1997), elevated predation and competition and reduced food availability for woodland-dependent birds (Andren 1992 , Zanette et al. 2000, Huhta et al. 2004, Maron et al. 2011).

The effects of clearing on habitat quality stem from the selective clearing of more productive parts of the landscape for agriculture (Vesk and Mac Nally 2006). In the woodlands of south-eastern Australia, the majority of the remnants are in areas of low primary productivity, and have often been heavily grazed, with much of the ground layer and understorey degraded. The lower productivity of the remnants lead to reduced food resouces for insectivorous birds (Watson 2011). The avifaunas of dry woodland systems of southern Australia continue to decline, due primarily to habitat loss compounded by a

range of other factors (Robinson and Traill 1996, Ford et al. 2001, Mac Nally et al. 2009, Ford 2011a), although the mechanisms generating these declines remain unclear.

The physiological status of individual birds may offer an insight into processes that vary in response to extent, configuration and condition of remnant habitat. Haematological and morphological measures have been used for assessment of individual condition (Norte et al. 2009a). Whole blood haemoglobin levels (Hb) and haematocrit (the ratio of packed blood cells to total blood volume, HCT) have been used to assess condition and physiological response in relation to habitat and to individual behaviour, such as reproductive investment and exercise levels (Campbell 1995). These measures have also been related to the effects of environmental stressors including parasite load, food availability and environmental toxins (Acquarone et al. 2002, Dudaniec et al. 2006, Linkie et al. 2006). Residual body mass (RBM), a measure of mass that accounts for structural size, is frequently used as an index of 'body condition' in ecological studies (Acevedo et al. 2005, Schulte-Hostedde et al. 2005, Stevenson and Woods 2006). It reflects variation in stored fuel reserves, particularly lipids, (Seewagen 2008), which have been shown to influence individual inclusive fitness in some birds (Ardia 2005).

HCT, Hb and RBM have been used to assess effects of environmental variation, including habitat fragmentation and habitat quality (and related food availability) on individual condition in wild passerines (Hõrak et al. 1998, Strong and Sherry 2000, Mazerolle and Hobson 2002) and small mammals (Johnstone et al. 2011). These three measures differ between sexes, and with reproductive status, age and season (Norte et al. 2009a), and RBM also varies with moult (Bojarinova et al. 1999). It is necessary to account for these covariates when investigating relationships between physiological condition and habitat. Where a relationship is found, further work is required to determine causality. The relationship may represent a direct effect of habitat on individual physiology; alternatively, individual condition may influence settlement choice (Porlier et al. 2009) or lead to competitive exclusion of individuals in poorer condition from favoured habitat (Latta and Faaborg 2002).

There has been much work assessing the impacts of changes in landscape composition and configuration on individual movement, gene flow and population genetics (Manel et al. 2003, Storfer et al. 2007). Less attention has been given to the influence of landscape

characteristics on individual genetic diversity, despite the important role that this quantity plays in evolutionary processes (Porlier et al. 2009). Population processes such as mating systems may be affected by changes in landscape structure and habitat condition (Banks et al. 2007) that could be reflected in individual heterozygosity levels (Garcia-Navas et al. 2009). Heterozygosity may be positively associated with offspring fitness, reproductive success, local survival and recruitment into the adult population (Coulson et al. 1998, Coltman et al. 1999, Coulson et al. 1999, Amos et al. 2001, Hansson et al. 2001, Banks et al. 2010), though meta-analysis of such heterozygosity–fitness correlations suggests that the effects are usually weak (Chapman et al. 2009). Such effects need not be restricted to sessile organisms; where mobile or dispersing individuals assess habitat quality before settling, fitter individuals (with higher individual heterozygosity) may choose and be able to defend higher quality territories (e.g. Seddon et al. 2004).

In addition to the individual-based responses to habitat alteration outlined above, disruption of natural patterns of mobility can lead to changes in population parameters, such as sex ratios or genetic diversity, with downstream consequences for individual and population fitness (Banks et al. 2007). For example, disrupted dispersal of the usual dispersing sex, females, in the Brown Treecreeper (*Climacteris picumnus*) in Australian woodlands, has been implicated in low female recruitment, isolated patches containing no females, and local patch extirpation (Cooper and Walters 2002, Cooper et al. 2002). Also, reduction in dispersal and gene flow, recent bottlenecks and/or disruptions of mating systems may lead to decreased levels of population genetic diversity (Palstra and Ruzzante 2008). Thus, associations of sex ratios and genetic diversity (measured by allelic richness; AR) with landscape conditions may provide evidence of important responses to landscape alteration.

The dry woodlands of south-eastern Australia have suffered considerable habitat clearance and degradation and there has been a corresponding and ongoing decline of the region's avifauna (Robinson and Traill 1996, Ford et al. 2001, Mac Nally et al. 2009). A pattern of disproportionately large decline in incidence in apparently suitable remnant habitat in many woodland-dependent birds compared to decline in landscape tree cover has been documented (Radford and Bennett 2007). Species showing this pattern of disproportionate decline have been termed 'decliner', while those that show no

relationship of incidence landscape tree cover have been termed ‘tolerant’ (Bennett and Radford 2009, Amos et al. 2012)

In this study, we examine the relationships of landscape structure and habitat condition with physiological status, individual and population genetic diversity and local sex ratio to explore whether these might be mechanisms underpinning some of the decline of resident woodland birds of south-eastern Australia. Specifically, we explore the possibility that there are impacts of landscape and site attributes on individual physical condition and heterozygosity, or on population genetic diversity and local sex ratios, that may be contributing to the observed pattern of decline through reduced individual and population condition and reproductive output, disruption of population processes, fitness and function (Hõrak et al. 1998, Kilgas et al. 2006).

We predicted that, if landscape and/or site condition are contributing to the decline of woodland-dependent birds in the study area, evidence of a relationship with RBM, HCT, or Hb should be found in the decliner species, and not in the tolerant species. Site condition is expected to affect sedentary species (those that stay in the same home range year round) more strongly than mobile ones, which may move locally or regionally between areas of varying condition. With regards to the effects of landscape and site on homozygosity-by-locus (HL), AR or sex ratio, evidence of differences related to landscape and site quality would support the hypothesis that population or social processes have been disrupted by change in habitat configuration or quality (Banks et al. 2007). Relationships between site and landscape variables and the response variables may also be due to condition-dependent settlement patterns. Nevertheless, the existence of differences in response variables relating to anthropogenic habitat change would be evidence of disruption of the birds’ interaction with their ecosystem.

5.2. METHODS

5.2.1. Site selection

This study built on the work of Radford et al. (2005), which examined the incidence of 58 species of woodland-dependent birds in 24 landscapes, each 10 × 10-km, in the woodlands of the Box–Ironbark region of central Victoria, Australia. Twelve 10 × 10-km landscapes were selected, nine of which were used by Radford et al. (2005). Tree cover in

these nine ranged from 10–50% and vegetation configuration in each was ‘dispersed’ or ‘aggregated’ (Radford et al. 2005, Radford and Bennett 2007). Three ‘reference’ landscapes were also selected. These had the highest available extent of tree cover (72–78%) to represent as near as possible the historical condition of continuous tree cover (Figure 1). Within all 12 landscapes, three to six sampling sites were selected, for a total of 63 sites (Figure 1).

5.2.2. Study species and sampling

We sampled 13 species of small to medium-sized resident woodland-dependent passerines. These species were the most frequently captured in the study area and represented a range of mobility and patterns of reduced incidence with respect to landscape-scale tree cover; either ‘decliner’, or ‘tolerant’ species (Table 1).

Fifty-seven sites were each visited twice in different seasons, with 4–7 months between visits. Sites were chosen opportunistically where there was a sufficient population of a number of the focal species for sampling to be viable. Six sites, where very few birds or only a single species were caught were not revisited. There were two days of sampling on each visit, between sunrise and 1 hour before sunset. Sampling occurred between November 2007 and February 2010, with the sampling of each landscape spread over this period. Birds were captured using 12 and 18-m, 31-mm-mesh mist nets 0.5–3 m above the ground. A secondary capture technique was used for ground-feeding birds: forty spring-loaded net traps (Reilly 1968) baited with mealworms and remotely monitored using UHF digital transmitters (Embedded Communications Systems, Launceston, Tasmania) were used mainly to catch Eastern Yellow Robin (*Eopsaltria australis*) and Grey Shrike-thrush (*Colluricincla harmonica*).

5.2.3. Bird attributes

Birds were aged and sexed from plumage and morphological characteristics following Rogers et al. (1986); the number of distinguishable classes varied from two (juvenile or adult plumage) to four (juvenile, hatchling, second and third year, and older) according to species. For 10 species, sex was confirmed genetically (below). Brown-headed Honeyeater, *Melithreptus brevirostris*; Buff-rumped Thornbill, *Acanthiza reguloides*, and Dusky Woodswallow were not sexed because they were not subject to a programme of

genotyping, and they could not be reliably sexed by plumage characters or other external characters (Rogers et al. 1986).

We measured total head-plus-bill length, bill depth at the base of the bill, tarsus length and wing chord to the nearest mm. Multiple blood samples (5–50 µl each) per bird were taken following brachial venepuncture with a 27-gauge hypodermic needle. Samples were collected into a heparinised microcapillary tube for HCT, a non-heparinised tube for genetic sampling and directly into a cuvette (Hemocue, Ängeholm, Sweden) for Hb. Blood samples for genetic analysis were transferred immediately into 1 ml of ethanol at ambient temperature in the field and −20ºC on return to the laboratory.

The HCT sample was spun for 4.5 min at 12,000 r.p.m. in a Zipocrit portable centrifuge (LW Scientific, Atlanta, Georgia, USA) with a haematocrit rotor. Total blood column length and packed cell length in the microcapillary tube were measured to ±0.5 mm.

Whole blood haemoglobin concentration was measured with a Hemocue 2001 B-Haemoglobin photometer (Hemocue, Ängeholm, Sweden) immediately after sampling. The value (g/dL) obtained by this method is higher than would be obtained by the standard cyanomethhaemoglobin methodology for avian blood (Eklom and Lill 2006, Simmons and Lill 2006). Given that our interest was in relative levels of Hb within species, the difference was inconsequential.

Ten species were genotyped for 6–16 polymorphic length-variable nuclear loci per species with a mean of 9.7 alleles per locus (s.d. = 8.0) (Appendix L). Assessment of all loci for departures from Hardy–Weinberg and linkage equilibria, sex linkage and null alleles showed that the genetic markers conformed to Mendelian expectations for codominant, autosomal loci without significant null allele frequencies (Harrisson et al. 2012, Pavlova et al. 2012, Harrisson et al. 2013). HL, which offers an efficient estimate of individual genetic diversity in populations with migration and admixture (Aparicio et al. 2006, Coulon 2010), was calculated across the pooled sample for each species using the R statistical package GenHet (Coulon 2010). Mean AR was calculated using R package HierFstat (Goudet 2005) for samples of >5 individuals for each species and mean AR was rarefied to the smallest included sample for a site.

Genotyped birds were sexed using sex-linked chromosome-helicase-DNA binding protein 1 (CHD1) gene. This gene has different-sized introns on the Z and W chromosomes, allowing homogametic (ZZ) males to be distinguished from heterogametic (ZW) females (Griffiths et al. 1998). PCRs for six species (Spotted Pardalote, Weebill, Eastern Yellow Robin, White-plumed Honeyeater, Yellow-tufted Honeyeater and Fuscous Honeyeater) were run separately as described in Harrisson et al. (2013). For Striated Pardalote, Grey Shrike- Thrush, Superb Fairy-wren and Brown Treecreeper the sexing reaction was incorporated into multiplex PCR (Pavlova et al. 2012, Harrisson et al. 2013). Individuals of known sex (Australian National Wildlife Collection samples) were used as positive controls on the first gels for each species. Each scored gel had clearly detectable Z and W bands. Polymorphism within CHD-Z and/or CHD-W, when detected, did not confound sex determination, as the difference between CHD-Z and CHD-W alleles was always much greater than that of two CHD-Z alleles (Pavlova et al. 2013).

5.2.4. Sample size

For some individuals, insufficient blood was collected to enable Hb or HCT to be measured; or processing time limited data collected. Hb samples were measured for 2525 and HCT for 2505 birds. For RBM (2239 individuals), only sexed adult birds (for sexed species) were analysed whereas all adults were included for Buff-rumped Thornbill, Brown-headed Honeyeater and Dusky Woodswallow. Sample sizes and numbers of sites and landscapes where each species was sampled are given in Table 2.

5.2.5. Landscape and site condition attributes

Landscape attributes included in the analysis were per cent tree cover (DSE 1990–1999) calculated in ARCGIS (ESRI 1999–2008) and configuration of tree cover: classified as aggregated, dispersed (Radford et al. 2005) or continuous (for the three highest cover landscapes). Site vegetation condition attributes were assessed using the Habitat Hectares methodology (Parkes et al. 2003), with raw data for each habitat component recorded. The Habitat Hectares method uses a measure of ‘deviation’ of the extant vegetation from an idealised structure for the vegetation at that location (Parkes et al. 2003). The area assessed at each site was the minimum convex polygon that included all net and trap locations. All vegetation condition assessments were carried out in the same season (17 August 2009–25 September 2009) and by the same individual (G. Sutter) to avoid

seasonal and observer differences in assessments (Gorrod and Keith 2009). Overall site condition scores (which have a possible value of 0–75 (Parkes et al. 2003) ranged from 12–52 (mean 41, s.d. 7.3).

A subset of these site condition data was used to calculate three variables we believed most likely to be related to individual bird condition. These were CANOPY, projected tree canopy cover (range 10–30% mean 19, s.d. 4.1); SHRUBS, the sum of projected cover of small (<1 m) medium (1–5 m) and large (>5 m) shrubs (range 0–58%, mean 27, s.d. 15.2); and LOGS, the length of fallen logs ha^{-1} (0–173 m ha^{-1}, mean 43, s.d. 35.3). LOGS value was log_{10}- transformed to improve normality of its distribution. Fallen logs form an important foraging resource for several of the target species, particularly the Brown Treecreeper (Noske 1979; Doerr , 2006)

Landscape context was used as a measure of connectedness of the vegetation at the site. Landscape context is a single index of the distance of a site from a large block of remnant vegetation and weighted vegetation cover within radii of 1, 3 and 5 km of the site (Ferwerda 2003, Parkes et al. 2003). Landscape context had a possible range of 0–100; values for the study sites ranged from 50–99 (mean 87, s.d 11.4).

5.2.6. Analyses

Principal component analysis (PCA) of wing chord, tarsus length, total head length and bill depth was conducted on standardised (zero mean, unit variance) values in R 2.13 (R Development Core Team 2011). A linear model of the first PCA regressed against mass was fitted. The difference of actual mass compared to the model was RBM. This analysis was carried out separately for each species, and for each sex in each species where sex was determined, as the relationship between size and RBM might differ between sexes (Green 2001)

We used generalised linear mixed models (GLMM) to assess evidence for effects of landscape and site variables. GLMM is useful for the analysis of data that are not normally distributed and where there are multiple random effects in large datasets (Bolker et al. 2009). The predictor variables were three landscape components (tree cover, landscape context and aggregation) and three components of vegetation condition at sampling sites (CANOPY, SHRUBS, and LOGS, as above). Models initially incorporated

spline functions (Lunn et al. 2009) to accommodate non-linear predictor effects, but we found no evidence of non-linear relationships and therefore present results of linear models only. Sine and cosine of ordinal day were included as fixed variables to account for seasonal variation in Hb, HCT and RBM. Both sine and cosine were used to contrast summer/winter and spring/autumn differences. The models fitted for Hb, HCT and RBM also included moult (presence or absence) as a random variable. Sex was included as a random effect for HCT and Hb for species where it was known. All models included landscape and site identity and year of capture as random variables. We used Gaussian errors for RBM, HCT, Hb, HL and AR models and a ninomial model structure for sex ratio (expressed as proportion of the more frequent sex).

We used Bayesian model selection with reversible jump Markov chain Monte Carlo (MCMC) sampling in WinBUGS (Lunn et al. 2000, Lunn et al. 2009) to identify landscape and site factors that were associated with each response variable, while accounting for sex, moult and seasonal effects. We modelled the entire sample for each species, subsamples for each sex, and for adults only. Inferences were made on posterior probabilities of inclusion in the best model for each candidate predictor variable. A posterior probability of inclusion >0.9 (corresponding to a posterior odds ratio of 10:1) is considered strong evidence that the variable is influential, and a probability >0.75 (odds ratio 3:1) is considered as 'substantial' evidence (Jeffreys 1961)

5.2.7. Model sensitivity

We used a dummy response variable to determine the capacity of models to detect influential variables, given our criterion for substantial evidence (probability of inclusion >0.75). We generated dummy response variables varying the correlation with a predictor variable. All other data were taken from the actual collected samples of four species (representing the range of sample sizes collected N = 60–250). From this we determined the minimum correlation between the predictor and dummy response variable that yielded a probability of inclusion >0.75. The capacity to detect a substantial effect increased with sample size (Figure 5). For species with substantial sample sizes (e.g. Brown Treecreeper), small effects (~5–6%) were detectible, whereas in species with small samples sizes (e.g. Weebill, Grey Shrike-thrush) effects would need to be large (~20%) to be detectable. If effects differed between sexes, a very large effect would be required if it were to be detected in species with small sample sizes.

5.3. RESULTS

5.3.1. Haematocrit, whole blood haemoglobin concentration and residual body mass

There was little evidence for relationships between landscape or site condition and Hb, HCT or RBM pooled between sexes. A single relationship for one species (Grey Shrike-thrush) was supported between cover of shrubs >1 m in height and HCT (R^2 = 0.09, probability of effect P = 0.82). All other effects were unsupported (P < 0.71; Appendix M). There was no support for any of the models when the sexes or adults alone were considered separately (results not shown).

5.3.2. Sex ratio and homozygosity-by-locus and allelic richness

Per-site sample sizes restricted the analysis of site AR to five species. We found little support for a relationship between AR and landscape or site condition. There was support only for a relationship between canopy cover and AR in the Fuscous Honeyeater (P = 0.78, Appendix N)

We found no support for inclusion of any of the landscape or site vegetation condition variables as predictors of skew in any of the study species (P < 0.66, Appendix O). There was no support for inclusion of landscape or site variables on HL in any species (P < 0.52, Appendix P), and no evidence of differences in HL between the sexes in any species (P < 0.9)

5.4. DISCUSSION

In only two of 389 combinations of species, responses and predictors was there support for an effect of landscape or site condition on individual body condition, levels of AR, HL or sex ratio skew. The study therefore provides little evidence that these effects contribute to the observed decline in woodland birds in the Box–Ironbark region.

Our simulations showed that the models used were capable of detecting moderate effects, R^2 > 0.2 with relatively small samples (N = 60) and very small effects with R^2 as small as ~0.05 with large (N > 250) samples. For a few species and response variables, sample sizes were too small to detect any but the largest effect (i.e. Hb and HCT in Weebill, and to a lesser extent in Buff-rumped Thornbill and Dusky Woodswallow). However, for the majority of tests, sample sizes were sufficient to detect an effect if it were present, either

for aggregate samples (204 tests where N >140), or in many cases also for individual sexes (Table 2).

While Hb, HCT and RBM have been identified as useful measurements for estimation of individual condition in relation to environmental factors (Campbell 1995, Norte et al. 2009a, Norte et al. 2009b), they are subject to variation due to age, sex, moult status and between season, year and time of day; breeding status and parasite loads also affect these measures (Hõrak et al. 1998, Ots et al. 1998, Fair et al. 2007, Norte et al. 2009a, Norte et al. 2010). Where used independently as indices of individual condition, these measures may lead to erroneous conclusions. HCT in particular has been challenged as an independent indicator of condition as it is affected by state of hydration (Dawson and Bortolotti 1997, Fair et al. 2007). Relationships of all three indices with individual condition are not monotonic, and similar values may be caused by positive or negative influences (Fair et al. 2007).

Nevertheless, a main aim of this study was to identify *any evidence* of an effect of our chosen site or landscape condition measures—which are widely used to describe landscape and habitat change—on Hb HCT, RBM, HL or sex ratio. We incorporated age, sex, moult status, season, and year into our models as random or fixed effects. We also modelled the two factors explaining the greatest variance—sex and age—separately. Despite the capacity of our analyses to detect small effects, we were unable to detect effects in the comparisons of interest (vegetation and individual condition) in this study.

Studies of the relationship between vegetation and individual condition in wild birds have produced differing results. Effects of habitat fragmentation in passerines have been shown to include elevated stress in chicks, and decreased RBM and HCT in breeding birds (Mazerolle and Hobson 2002, Suorsa et al. 2003a), and Hb level in chicks and RBM in adults may relate to food availability (Strong and Sherry 2000, Banbura et al. 2007). No relationship was found between landscape forest cover and RBM for some overwintering birds (Tellería et al. 2001, Turcotte and Desrochers 2008).

The studies showing an effect of fragmentation on individual condition mostly examined breeding individuals or their nestlings. Studies restricted to nestlings, or specifically to birds of known breeding status (Suorsa et al. 2003a, Suorsa et al. 2003b, Norte et al. 2009b, Norte et al. 2010) allow the removal of the effects of age and reproductive status

from analysis. They offer more sensitive probes of response to vegetation variables. Such studies are likely to be limited to single species readily sampled at the nest, or intensive studies of marked populations. Our study attempted a more general, multi-species approach, sampling many sites without repeated sampling of individuals. We could estimate age only from plumage, and could not be sure of the breeding status of birds, unless they had a marked brood patch, and therefore had limited ability to account for age and breeding status *per se*.

The region in which the study was undertaken was under extreme climatic stress at the time of the study, having suffered one of the most extreme droughts worldwide from 1997 to 2010 (Leblanc et al. 2009). Although earlier studies recorded declines in avifauna related to area of remnant tree cover in the landscape (Lindenmayer and Fischer 2007), the more recent reports found that decline in numbers was occurring across the region regardless of amount of remnant tree cover (Mac Nally et al. 2009). These declines were found across all foraging guilds, including the nectarivores and insectivores of our study. The declines were probably due to reduced food resources (Mac Nally et al. 2009). This may have led to a uniform degree of stress across the entire region, so that effects of landscape configuration or in-site vegetation would be difficult to ascribe. Turcotte and Desrochers (2008) argued that the lack of effect of habitat fragmentation on body condition may be due to differential mortality, predation, or attempted emigration of individuals in poorer condition from fragments. Such a mechanism may explain the lack of effect in our system, although Turcotte and Desrochers' (2008) birds were subject to regular seasonal stresses rather than the longer term set of stresses caused by drought in our study system, albeit also causing reduced food abundance, and potentially reduced breeding (Mac Nally et al. 2009). There is a paradox here: if all except the best-conditioned birds are absent from localities (or indeed a whole region due to intrinsic attributes of the individuals), then it may not be possible to detect the effect in the birds themselves, since the poorer conditioned individuals are absent. The result may be fewer birds remaining; that is, the decline in occurrence observed (Radford and Bennett 2007, Mac Nally et al. 2009) with the proximate cause of the decline no longer apparent because the poorer condition birds are absent.

A second factor that may have reduced our ability to detect an effect was the small range of habitat condition in sites that were of sufficient quality to contain woodland-dependent

birds. Habitat scores (Parkes et al. 2003) for sample sites had relatively little variation (12–52 out of a possible 75). Most sites had a similar level of degradation: there were no sites in very good condition, and only a few in exceptionally poor condition. Broad modelling of vegetation condition across the State of Victoria showed that the majority of our sites were at the upper end of the available range of condition (DSE 2008). Our sampling sites, of necessity, were located where sufficient birds were present to make sampling practical; most sites in very poor condition had few woodland-dependent birds present.

Our results indicate that the commonly used measures of avian condition considered here are not useful for discerning the effects of landscape and vegetation change for woodland-dependent passerines. Moreover, there is little evidence that stress *per se*, at least as indicated by these condition measures, is responsible for the decline or otherwise of the woodland birds. There were good grounds for expecting differences, especially between decliner and tolerant species and between sedentary and mobile species, given the rich background of data from prior work. We had substantial capacity to discern effects of stress were these were important.

Table 10: Classification of studied species according to their response to tree cover and their expected mobility

Species that were sexed and genotyped are highlighted in bold.

Table modified from Amos et al. (2012)

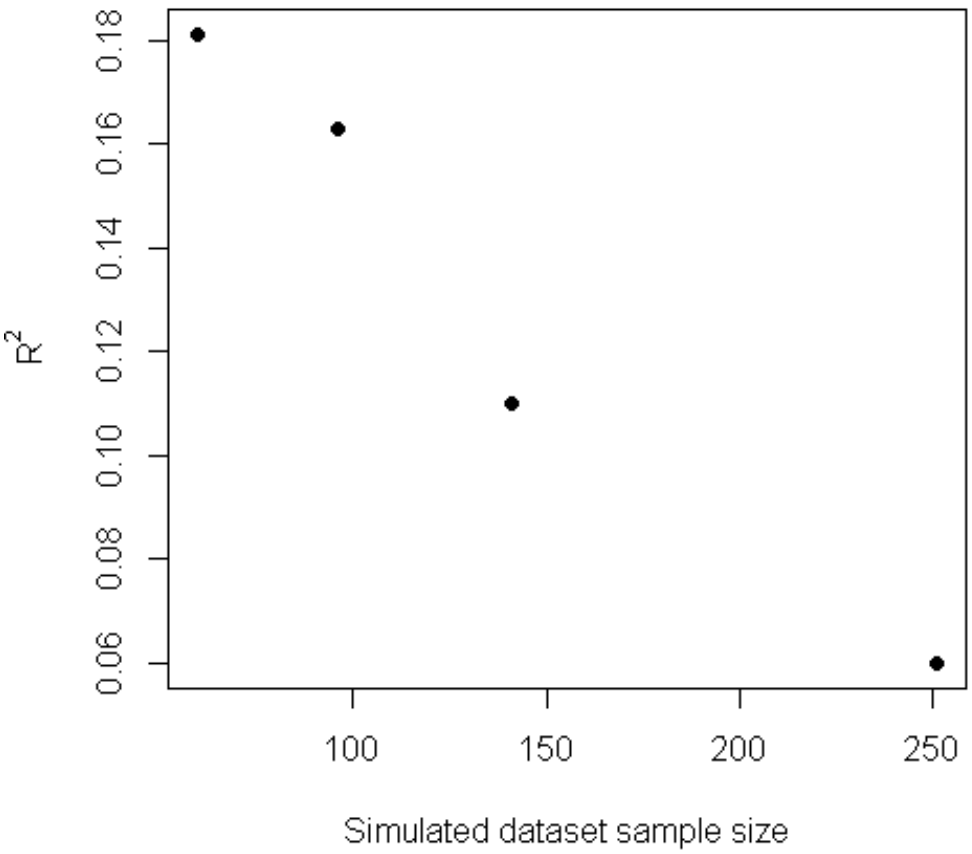
Mobility	Response to landscape tree cover	
	Decliner	Tolerant
Mobile	**Fuscous Honeyeater (*Lichenostomus fuscus*)** Dusky Woodswallow (*Artamus cyanopterus*) Brown-headed Honeyeater (*Melithreptus brevirostris*)	**White-plumed Honeyeater (*Lichenostomus penicillatus*)**
Moderate/ inconclusive[1]	**Yellow-tufted Honeyeater (*Lichenostomus melanops*)** **Spotted Pardalote (*Pardalotus punctatus*)** **Grey Shrike-thrush (*Colluricincla harmonica*)** **Weebill (*Smicrornis brevirostris*)**	**Striated Pardalote (*Pardalotus striatus*)**
Sedentary/ inconclusive[1]	**Eastern Yellow Robin (*Eopsaltria australis*)** **Superb Fairy-wren (*Malurus cyaneus*)** Buff-rumped Thornbill (*Acanthiza reguloides*)	
Sedentary	**Brown Treecreeper (*Climacteris picumnus*)**	

[1]For mobility, the term 'inconclusive' is used where there is uncertainty about mobility levels from the literature (Higgins et al. 2001, Higgins and Peter 2002).

Table 11: Sample size for each response variable in each species for adults and total by sex and number of sites and landscapes where each species was sampled

	Haematocrit								Total blood haemoglobin								Residual body mass					
	Female		Male		Unsexed		Totals		Female		Male		Unsexed		Totals		Male	Female	Unsexed	Total	No. Sites	No. Landscapes
Species	Adults	All	Adult	All	Adult	All	Adult	All	Adult	All	Adult	All	Adult	All	Adult	All	Adult	Adult	Adult	Adult		
Brown Treecreeper	158	207	189	235			347	442	173	224	199	243			372	467	175	206		381	48	12
Eastern Yellow Robin	33	39	49	60			82	99	33	40	52	63			85	103	43	63		106	32	12
Fuscous Honeyeater	116	158	192	237			308	395	115	163	185	230			300	393	142	218		360	41	12
Grey Shrike- thrush	20	38	33	51			53	89	21	38	32	49			53	87	20	32		52	39	12
Superb Fairy-wren	52	59	74	80			126	139	57	66	67	73			124	139	63	93		156	33	12
Spotted Pardalote	16	35	19	41			35	76	12	33	16	39			28	72	17	13		30	13	9
Striated Pardalote	41	90	66	115			107	205	37	82	72	118			109	200	53	78		131	32	12
Weebill	7	7	20	21	2	2	29	30	10	10	18	19	1		29	29	20	45		65	22	11
White-plumed Honeyeater	73	77	201	212	96	125	370	414	77	81	209	221	100	126	386	428	81	224		305	40	11
Yellow-tufted Honeyeater	128	160	222	251		1	350	412	121	157	216	244		2	337	403	144	249		393	28	11
Brown-headed Honeyeater					82	97	82	97					83	97	83	97			104	104	20	9
Buff-rumped Thornbill					53	53	53	53					54	53	54	53			92	92	33	12
Dusky Woodswallow					54	54	54	54					51	54	51	54			64	64	24	11

Figure 5: Minimum R^2 required in simulated dataset for an effect to be detected of $P > 0.75$



6. DISCUSSION AND CONCLUSIONS

6.1. MAIN AIMS AND THE PROJECT CONTEXT IN WHICH THEY WERE ADDRESSED

I set out to establish whether reduced structural connectivity and/or vegetation condition in the fragmented woodlands of central Victoria was a cause of the observed decline in some of the woodland-dependent birds of the area. To do so I established a methodology to predict and compare relative effects of fragmentation across multiple species, based on their published response to landscape-level tree cover, the available limited information on relative mobility and dispersal of each of the species (Chapter 2), and tested these predictions using genetic data (Chapter 4).

My study formed part of a large project 'Birds in Fragmented Landscapes', which resulted in a number of publications not included in this thesis but on which I was a co-author. Whereas my thesis focused on the comparison of the effects of fragmentation across all the species sampled, several other studies from the project incorporated the spatial models I developed when considering population genetics responses of focused subsets of the test species (Harrisson et al. 2012, 2013, 2014). The analyses in these studies, in turn, refined my work through the identification and exclusion of progeny of the cooperatively breeding Superb Fairy-wren and Brown-Treecreeper (Pavlova et.al. unpublished) from landscape genetics analyses, the identification of the east–west split in our study landscapes and identification of sex-specific fragmentation effects (Harrisson et al. 2012, Amos et al. 2014). I also applied my spatial models to address other aspects of impacts of habitat alteration in the birds we sampled, notably song type similarity across the space of the Grey Shrike-thrush in relation to structural connectivity in the study area (Pavlova et al. 2012), and perpendicular mitochondrial and nuclear phylogeographic patterns in the Eastern Yellow Robin across its range (Pavlova et al. 2013). The relevance of my contributions to these additional publications is incorporated into the summary of novel approaches and findings of the study (Table 12).

6.2. INSIGHTS INTO THE RELATIVE PERFORMANCE OF CIRCUIT DISTANCE AND LEAST-COST PATH, APPLIED TO BIRDS

Comparison of the results of LCP and CS connectivity algorithms in real landscapes (Chapter 3) identified the importance of the choice of the appropriate null model to match as closely as possible the form of the IBD response for the algorithm used. The shape of the IBD response also differs with choice of genetic distance and will in turn influence the choice of an appropriate null (Graves 2012). Further, I found that the apparent shortcoming in the calculation of CS in Circuitscape (McRae and Beier 2007)—an 'edge effect' that necessitates buffering of the study area (Koen et al. 2010)—may in fact allow the algorithm to simulate the effect of heterogeneous landscapes better. CS achieves this through better simulation (compared to LCP) of IBD in the irregular patches of different resistance composing a heterogeneous landscape, and integration of these multiple patches of different IBD gradients ('patchy IBD', Chapter 3). In this study I found that CS was a stronger predictor than LCP of individual genotypic distance (Smouse and Peakall 1999) and pairwise population $F_{ST.}$ This was the first study to compare LCP and CS in flying animals. The relatively high mobility of birds compared to many organisms previously studied may explain the difference between my finding that CS was predominantly a better model than LCP, and the outcomes of several other studies. Because birds are able to fly across cleared areas, and also to consider shorter crossings literally from a bird's-eye view (e.g. to see a fragment of tree cover at greater distance), they may be in a position to choose straighter and faster paths even where these have a higher resistance. CS in essence aggregates the potential contribution that many of these apparently sub-optimal paths may contribute to the probability that an individual will move between fragments.

6.3. EXTENT OF FRAGMENTATION EFFECTS ON BIRDS IN VICTORIAN BOX–IRONBARK HABITAT

Evidence of the impact of fragmentation on gene flow and individual dispersal was generally weaker that we had predicted, with IBR being detected in only half of the species for which it was predicted. Some evidence of fragmentation effects was found in a further species by other studies from the project on which I was a co-author. For example, by applying

'landscape bioacoustics' we were able to demonstrate the disruption of social processes in the absence of genetic evidence of decreased dispersal. In the Grey Shrike-thrush, a 'decliner' species for which we had predicted IBR, genotypic distances were not structured according to IBR, but song type similarities supported a model of impairment of cultural (acoustic) connectivity through cleared areas (Pavlova et al. 2012). Evidence for disruption to diverse aspects of biology including local relatedness structure, sex ratios and mating systems was seen in a high proportion of other species examined (Harrisson et al. 2012, 2013). Therefore, it is reasonable to assume that such impacts of fragmentation are common. Thus, in addition to the fact that we were not able to examine all aspects of species biology, I am confident that our analyses underestimate the impacts of habitat fragmentation on Box–Ironbark birds because the study was necessarily focused in landscapes with at least moderate tree cover. The only way to conduct population genetics on patches from which a species is extirpated would be to have samples collected from the period after the birds began to be impacted but before they had disappeared; which were not available. Such samples would be very important resources for ecologists and wildlife managers to assemble.

Despite the weaker and less frequent evidence than expected of IBD in decliner species, the pattern of effects was clear, with IBR being detected in the least mobile (though still relatively mobile) honeyeater species (Yellow-tufted Honeyeater), and the three least mobile species (where the effects were predicted to be strongest). Interestingly, these three species are also the only cooperatively breeding species in the study, suggesting cooperatively breeding species may be relatively vulnerable to the effects of fragmentation. We were careful to reduce the effects of group structure in these species, through the identification and removal from connectivity analysis of all progeny at the same site as their parent(s) (Harrisson et al. 2013, Amos et al. 2014). Unfortunately, I was unable to sample the White-winged Chough (*Corcorax melanorhamphos*), the one sedentary but 'tolerant' cooperative breeder identified by Radford and Bennett (2007), and therefore could not test for differences in isolation mechanisms between sedentary tolerant and declining species. It is a much larger bird than any of the study species and would have required specialised and time-consuming capture techniques that were not feasible in our multi-species sampling programme.

A notable fragmentation effect was sex-specific IBR in Brown Treecreeper and Superb Fairy-wren. Both species exhibit female-biased dispersal (Noske 1991, Mulder 1995), yet the responses to fragmentation differed between the two, with IBR being apparent in female Brown Treecreepers and male Superb Fairy-wrens. The IBR evident in female Brown Treecreepers would have been missed if the sexes had not been considered separately, since strong IBD in males masked the effect. Although sex-specific dispersal differences were also detected in Eastern Yellow Robin, Yellow-tufted Honeyeater (exhibiting male philopatry) and Grey Shrike-thrush (female philopatry), sex-specific IBR effects were not demonstrated. However, the sample sizes of Eastern Yellow Robin and Grey Shrike-thrush were sufficiently small to plausibly have limited the ability to detect such effects (Harrisson et al. 2012, 2014, Pavlova et al. 2012). Given the likely prevalence of sex-specific fragmentation effects and their potential to go undetected if not specifically sought (Shanahan et al. 2010, Amos et al. 2014), I emphasise that landscape connectivity studies should test for differences in landscape effects between sexes. This is important because IBR in either sex will likely affect the viability of isolated populations.

6.4. Fragmentation results in alterations of a complex range of genetic, demographic and social processes

My study focused on the effects of functional connectivity for dispersal and gene flow—that is, the combination of dispersal outside the natal range—and subsequent reproduction. Strong differences were found between sedentary species, which showed genetic evidence of decreased landscape connectivity in fragmented landscapes, and the more mobile species that did not show this effect. This is not inconsistent with studies of gap crossing and local foray behaviour that show similar gap-crossing behaviour between sedentary and more mobile or nomadic species, because those movements relate to day-to-day local patterns, not nomadic or migratory events (Robertson and Radford 2009, Doerr et al. 2011). Nonetheless, similarly to Doerr et al. (2011), this study identified the importance of scattered paddock trees <100 m apart in the maintenance of functional connectivity for Brown Treecreepers, suggesting that this habitat element is important in breeding dispersal movements as well as short-distance forays.

The complexity of the effects of fragmentation and reduced connectivity is apparent in the range of responses by the sedentary and less mobile species studied. In addition to the direct effects of reduced dispersal and gene flow on demographic viability of populations of these species, other more subtle effects including changes in sex ratios and in acoustic connectivity, may lead to disruption of social structures in fragmented habitats (Laiolo and Tella 2005, Banks et al. 2007).

Evidence of IBR in the least mobile of our study species, weak IBR in the moderately mobile Yellow-tufted Honeyeater, and the absence of any detectible IBR or IBD in the more mobile species suggest a continuum of individual species responses to fragmentation. The observation of Ford (2011b), that there appear to be two broad patterns of extinction debt in the declining birds of Australia's temperate woodlands, reflect the ends of this continuum. At one extreme, less mobile species suffer from reduced effective connectivity, inability to recolonise patches and 'twinkling out' as they disappear from one remnant, then another. At the other end of the spectrum, the most mobile honeyeaters are well able to recolonise patches, but are nevertheless declining across parts of their range ('dimming down', Ford 2011b), perhaps as a result of declining availability of nectar resources at critical times, due to selective loss of the more productive patches in the landscape, drought and/or climate change (Mac Nally et al. 2009, Ford 2011a, Watson 2011). Species such as the Yellow-tufted Honeyeater and perhaps the Grey Shrike-thrush are positioned somewhere between these extremes, with restrictions to mobility as well as scarcity of critical resources causing their decline.

6.5. LANDSCAPE GENOMICS: MORE RESOLUTION WITHOUT MORE SAMPLING

This study undertook intensive sampling across members of a community at a scale that has not been matched by other studies. Nevertheless, our ability to detect genetic structure was limited by the achievable sample sizes, and the number of localities that could feasibly be sampled. Part of the issue here was that half of our study species appeared to be more mobile than expected. Thus, any evidence of spatial structure in those species would be relatively weak on the scale of the study, thus requiring more sample sites, individuals and/or loci to detect an effect. A weak effect was found for the Yellow-tufted Honeyeater, a species for

which we had a very large sample size (N = 471). Simulations have shown that the increase in power of landscape genetics inferences from more loci exceeds that from more individuals (Landguth et al. 2012). 'Next-generation' genomics is providing increases of orders of magnitude in the number of loci, with thousands of single nucleotide polymorphisms, compared to the 10–20 loci of 'current generation' landscape genetics (Allendorf et al. 2010). The power of the these techniques, now being widely adopted, will allow more reliable individual- and population-level measures from modest numbers (4–6) of individuals per population. It will also allow detection of spatial structure (and IBR) in more mobile species (Anderson et al. 2010). The greatly increased resolution available through landscape genomics will also allow analyses currently of limited utility and resolution with genotypes of 10–20 loci typical of microsatellite studies. The identification of near relatives will increase in confidence and be applicable over larger distances, and effective population sizes and rates of immigration and emigration might be able to be estimated more accurately (Allendorf et al. 2010, Xing et al. 2010). These approaches may allow the complexity of inter-patch and metapopulation movements of individuals to be inferred in greater detail and enable more detailed analyses of landscape connectivity, perhaps enabling us to determine more easily which particular connections are of most importance and how frequently they are used. We would then be able to provide more detailed prescriptions of the attributes of revegetation that will provide the greatest benefit in reconnecting landscapes.

The gain in landscape genetic resolution from next-generation techniques is important because it is unlikely that efficiency of obtaining genetic samples for wild vertebrates is going to increase dramatically. This is particularly acute for non-lethal sampling of birds, for which there is currently no equivalent of electrofishing, nor a biopsy gun. In this study I trialled imaginative methods to increase capture success, including various designs of traps, nesting boxes, decoy birds, artificial nectar feeders and water as 'bait' in dry periods (details not reported in this thesis). Although possibly somewhat effective for some species in some circumstances, these innovations did not materially increase capture success across the board, and mist netting apparently remains the best non-lethal way to obtain a broad sample of species of woodland birds. The logistics and work associated was increased in the present study by routine incorporation of enhancers such as call playback, and the many precautions

we built in to protect the birds' welfare. Thus, while effective, mist netting is time demanding and imposes limits to the number of sites that can be surveyed. Hence, large-scale multi-species studies will continue to require extensive field sampling, or to be based in those areas where samples have fortuitously been collected and preserved as part of other studies, from the relevant part of the population's trajectory. It would certainly be useful to revisit the samples collected for this project with next-generation techniques: projects at similar scales are unlikely to be able to be undertaken often within current national and state priorities. Although emerging genetic technology makes it likely that there will be much better resolution to estimate mobility and gene flow and other population parameters, it is still reliant on widespread field sampling to be most informative. Thus, is it extremely important for field biologists to collect genetic samples whenever the opportunity arises as part of any studies involving capture of wildlife. These opportunities are extremely valuable financially, and irreplaceable as a record of that point in history. Given the negligible additional stress of collecting minute tissue samples, compared to the overall stress of capture and handling on the animals, it seems almost negligent for biologists not to extract the full value possible from their fieldwork. These *ad hoc* collections, if properly registered and deposited within public collections, will allow temporal comparisons to detect demographic change over time in species which currently lacking data on population trends.

6.6. NEED FOR NEW APPROACHES TO LANDSCAPE GENETICS STATISTICAL ANALYSES AND INCREASED INTEGRATION OF SIMULATION APPROACHES WITH ANALYSES OF FIELD DATA

Although landscape genetics is now maturing as a discipline, there is still need for the development of statistical approaches that deal better than do Mantel tests with relationships among multiple pairwise distances and/or correlated landscape variables. The Mantel and partial Mantel tests, often coupled with a causal modelling framework, remain the most accepted approach to testing landscape genetic hypotheses that are dependent on the comparison of multiple distance matrices. Nevertheless, it is recognised that their power is limited (Legendre and Fortin 2010, Cushman et al. 2013). Modifications to the causal modelling framework approach, including those used in this thesis, have been suggested to

maximise the inferences that can be made (Wasserman et al. 2010, Cushman et al. 2013, Amos et al. 2014: Chapter 4), but the approach has reached its limits. New techniques, independent of the assumption of a linear relationship between genetic and landscape distances are required to move forward, particularly in analyses involving individual genetic distances where the relationships are neither linear nor log-linear, and may asymptote at a distance related to the maximal dispersal distance of the study subject (Graves 2012). One recently suggested novel approach that may show a way forward is Bayesian estimation of differentiation in alleles by spatial structure and local ecology (Bradburd et al. 2013a). At the moment its efficacy has been demonstrated with single nucleotide polymorphism counts between populations (not individual genetic distances); this approach would be more accessible if it can be framed in a suitable model selection procedure to allow more rigorous comparison of alternative landscape or ecological distance scenarios, for which it will require extensive validation. A second approach that may be worthy of consideration is development of generalised dissimilarity modelling, though, again, in its current form it does not offer a straightforward comparison of competing distance models (Ferrier et al. 2007, Thomassen et al. 2010).

An alternative way forward may be further use of connectivity measures that are site-wise rather than pairwise. This has the advantage of removing the statistical limitation imposed by pairwise comparisons and multiple distance matrices; however, it removes the consideration of particular connections in the landscape. Site-wise connectivity measures have already been used, either by considering mean connectedness of one site to all other sites of interest, or through the use of resistant kernel methods (Compton et al. 2007, James et al. 2011). It is now computationally feasible to calculate resistant kernels over landscapes represented by millions of pixels; the ability will be included in a forthcoming release of FRAGSTATS (McGarigal et al. 2012, McGarigal 2014). This will facilitate the use of site-wise connectivity models for more mobile taxa such as birds, in landscapes of the size and complexity studied in this thesis.

In the last few years, spatially explicit individual population genetics simulations have been used to test and confirm some basic assumptions of landscape genetics in simulated landscapes and for a few relatively simple actual landscapes (Cushman and Landguth 2010,

Landguth et al. 2010a, 2010b, Jaquiéry et al. 2011, Oyler-McCance et al. 2012, Cushman et al. 2013). These have simulated IBD, IBR and isolation-by-barrier mechanisms under a range of assumptions, with different dispersal and demographic parameters, with the aim, among others, to determine the ability of current statistical techniques to correctly identify causal landscape genetics processes (Cushman et al. 2013). I attempted such simulations for our study area. Computational resources and time limited the simulations to individual 10 × 10 km landscapes (with a notional 10,000 individuals in the null, 'all habitat' landscape. Despite the unusually large data set, we had insufficient genetic data to allow comparison of actual genetic distance for these simulations (J.N. Amos and B.K. Hand unpublished data). Given our limited understanding of the population genetic patterns arising from various spatial isolation processes, particularly on individual genotypic distances, there is a need to continue this work, accounting for more of the parameters that may affect the patterns that develop; for example, overlapping generations, fluctuations in population size, local extinctions and recolonisations of patches (Balkenhol and Landguth 2011, Graves 2012, Landguth et al. 2013). As the efficiency of simulations (and, therefore, the ability to deal with larger numbers of individuals and complexity of the landscape model rasters) improves, simulations of realistic populations should be used in study landscapes. This would allow construction of more accurate null models and alternative models of effects of heterogeneous landscape connectivity on genetic patterns and establish the reliability with which analyses are able to distinguish among alternative connectivity models (Graves et al. 2013), which remains a key concern around these approaches. The simulated genetic results could then be compared with observed patterns from genetic samples in the study landscape to determine the best model of actual genetic connectivity.

The period of this study coincided with the latter part of a major period of drought in south-eastern Australia, the so-called 'Big Dry', depressing abundance and, thus, sample sizes for all of our study species. Breeding of many species assessed at that large scale was also limited (Mac Nally et al. 2009). This additional, extreme stressor on an already-declining community may partially explain the lack of any differences in individual condition related to landscape context or generic measures of vegetation condition (Amos et al. 2013: Chapter 5). Few of our target species have shown resilience through population recovery in the two

wet seasons that followed the drought; although, with only two breeding seasons of data post-drought, it may still be too early to tell if the less fecund species are recovering (Bennett et al. 2014).

6.7. CONCLUSION

In conclusion, my study demonstrated that among the declining woodland birds of south-eastern Australia, movement of some species with the lowest mobility is constrained by habitat fragmentation, in some cases this effect is sex specific (Harrisson et al. 2013, Amos et al. 2014), and there is some evidence of weaker effects of fragmentation in species of intermediate mobility (Pavlova et al. 2012, Amos et al. 2014, Harrisson et al. 2014). Although there still appears to be sufficient gene flow in the more mobile sex to prevent deleterious effects of inbreeding and loss of genetic diversity in the fragmented populations, there is clear evidence of the disruption of population processes and potentially insufficient among-subpopulation dispersal to maintain demographic connectivity, and thus viability, of small subpopulations (due to lack of recolonisation of patches where stochastic processes have led to local extirpation). The most mobile of our study species showed no sign of disrupted dispersal ability (Harrisson et al. 2012, Amos et al. 2014, Harrisson et al. 2014), so the declining mobile species must be experiencing other impacts such as decreased critical resource availability, increased competition, exclusion and climate change (Grey et al. 1997, Mac Nally et al. 2009, Ford 2011a, Watson 2011, Bennett et al. 2014a, 2014b). Thus for any species we can envisage a continuum of fragmentation impacts, with different, probably interacting contributions of these other processes resulting in the patterns observed by Ford (2011b). Nevertheless, to minimise the extinction debt paid through continued decline and loss of the majority of bird species, it is essential that land managers address both the enhancement of connectivity between remnants (to improve the viability of the less mobile species that are being impacted on by decreased connectivity in fragmented habitat), and the improvement of the condition of existing remnants. This will entail reconstructing habitat in more productive parts of the landscape, where clearing has been most complete (to improve the viability of the more mobile species, currently ‘dimming out’ across the woodlands). The combination of these restoration measures may also partially address the requirements of those decliners that sit somewhere between these two extremes.

Table 12: **Summary of contributions made as part of this thesis and in related publications of which I was a co-author**

Novel approach or finding	**Implications**	**Future directions/challenges to solve**
Multi-species/suite landscape genetic comparisons across same sites and landscape (Chapter 2: Amos et al. 2012).	Allows inferences to use a comparative approach contrasting species based on differences in mobility and observed response to proportion of landscape remnant tree cover. Framework for prior prediction of landscape genetics response by ranking strength of correlation to landscape connectivity models.	Intensive sampling requirements—limitation to species that can be sampled using single efficient methodology that can be applied in many sites (to reduce local genetic autocorrelation of samples). Responses were weaker than expected, requiring modification of prediction framework (Chapter 4: Amos et al. 2014).
Least-cost path *vs*. circuit distance comparison, across species in same landscape (Chapter 3).	The greatest number of species used in comparison to date. First comparison of flying organisms.	Limited strength of isolation-by-resistance (IBR) in the study prevented definitive conclusions. Need for increased use of spatially explicit simulations to better understand individual genotypic distance responses and population responses in complex landscapes. The need for current individual-based simulations to rely on one of the effective distance modelling approaches as an input to describe gene flow patterns leads to a circularity.

Novel approach or finding	**Implications**	**Future directions/challenges to solve**
Modification of causal modelling framework (CMF) with Mantel tests to maximise ability to distinguish IBR from IBD, by selecting the best IBR model from a plausible range and comparing this with IBD (Chapter 4: Amos et al. 2014).	Maximised inferences possible given weaker than anticipated landscape genetics signal in our study system.	CMF has reached its limits. Need for novel statistical approaches (Ferrier et al. 2007, Bradburd et al. 2013b). Reduction of pairwise (distance) to site-wise measures resistance kernels to allow the use of analyses such as redundancy analysis (Dixon 2003, Oksanen et al. 2012) to separate multiple correlated environmental and geographic parameters (e.g. Pavlova et al. 2013).
Extensive comparison of isolation effects between sexes (Harrisson et al. 2013, Amos et al. 2014).	Sex-specific fragmentation effects. Able to fit observed pattern to observed local decline and extinction in Brown Treecreeper due to disappearance of females from isolated patches. Male-only IBR in Superb Fairy-wren related to mating system and social structure of this species (Harrisson et al. 2013).	Highlighted need to consider sexes separately to avoid isolation-by-distance (IBD) masking IBR in dispersing sex in sedentary species.
Impacts of sample sizes. Weak IBR detected in Yellow-tufted Honeyeater (a mobile species) possible due to large sample size (Amos et al. 2014, Harrisson et al. 2014). Weak, population-level effect found in sedentary Eastern Yellow Robin, with relatively small sample size.	Even some more mobile birds (such as the Yellow-tufted Honeyeater) may be subject to decreasing population connectivity following fragmentation. This can only be determined using current techniques where very large sample sizes are available.	Revisit these species with increased power of a landscape genomics approach to confirm and further resolve effects.

Novel approach or finding	**Implications**	**Future directions/challenges to solve**
High gene flow in decliner and resister congenerics. Absence of expected spatial genetic structure in both pardalotes and two honeyeater species (Chapter 4: Amos et al. 2014).	Lack of evidence of IBR corroborated by findings of broader scale homogeneity and lack of marked within-landscape spatial autocorrelation in parallel work (Harrisson et al. 2012, 2014).	Need to use a number of approaches in conjunction, to identify disruptions not apparent in genetic differentiation. The level of dispersal required to prevent genetic differentiation is markedly less than that required for demographic connectivity (Lowe and Allendorf 2010). Increased power of assignment and identification of relatives with genomic datasets may allow better estimates of the frequency of movement between remnants.
Consideration of scale/different areas—different processes may occur. Contrasting patterns of genetic structure within landscape study area, east *vs.* west.	Need to consider the possibility of multiple genetic structures across a study area, and the role of recent historic environmental patterns in determining genetic structure.	
Demographic *vs*. genetic connectivity. Evidence of fragmentation disrupting social connectivity where genetic disruption was not evident (Pavlova et al 2012).	Two significant innovations were trialled in this study of the effects of fragmentation on genetic and social connectivity of a sedentary decliner, the Grey Shrike-thrush. First, in addition to testing models of decreased mobility, we also tested the models of increased mobility through non-habitat. Second, we applied landscape bioacoustics to test various mobility models using song dissimilarities across the study area.	

Novel approach or finding	Implications	Future directions/challenges to solve
Integration of individual fitness/condition measures. Large multi-species dataset of body condition, haematological stress indicators collected as collateral benefit of genetic sampling—allowed testing for some alternative processes that may have been causing species decline (Chapter 5: Amos et al. 2013).	No effects found—suggests that individual condition measures were not useful indicator of decline and/or that landscape processes, not individual site-condition processes, are the drivers.	Conducted during the 'Big Dry'—may be that all surviving individuals were at similarly high stress levels. Given the size of the dataset it may be worth resampling in more favourable conditions to determine whether haematological and body condition indices in surviving birds in the Big Dry were universally depressed.

REFERENCES

Acevedo, P., M. Delibes-Mateos, M. A. Escudero, J. Vicente, J. Marco, and C. Gortazar. 2005. Environmental constraints in the colonization sequence of roe deer (Capreolus capreolus Linnaeus, 1758) across the Iberian Mountains, Spain. Journal of Biogeography **32**:1671-1680.

Acquarone, C., M. Cucco, S. L. Cauli, and G. Malacarne. 2002. Effects of food abundance and predictability on body condition and health parameters: experimental tests with the hooded crow. Ibis **144**:E155-E163.

Adriaensen, F., J. P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning **64**:233-247.

Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews Genetics **11**:697-709.

Amos, J. N., A. F. Bennett, R. Mac Nally, G. Newell, J. Q. Radford , A. Pavlova, J. Thompson, M. White, and P. Sunnucks. 2012. Predicting landscape genetic consequences of habitat loss, fragmentation and mobility for multiple species of woodland birds. PLoS ONE **7**:e30888.

Amos, J. N., S. Balasubramaniam, L. Grootendorst, K. A. Harrisson, A. Lill, R. Mac Nally, A. Pavlova, J. Q. Radford, N. Takeuchi, J. R. Thomson, and P. Sunnucks. 2013. Little evidence that condition, stress indicators, sex ratio, or homozygosity are related to landscape or habitat attributes in declining woodland birds. Journal of Avian Biology **44**:45-54.

Amos, J. N., K. A. Harrisson, J. Q. Radford, M. White, G. Newell, R. M. Nally, P. Sunnucks, and A. Pavlova. 2014. Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds. Ecology **95**:1556-1568.

Amos, W., J. W. Wilmer, K. Fullard, T. M. Burg, J. P. Croxall, D. Bloch, and T. Coulson. 2001. The influence of parental relatedness on reproductive success. Proceedings of the Royal Society B: Biological Sciences **268**:2021-2027.

Anderson, C. D., B. K. Epperson, M.-J. Fortin, R. Holderegger, P. M. A. James, M. S. Rosenberg, K. T. Scribner, and S. Spear. 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology **19**:3565-3575.

Andren, H. 1992. Corvid Density and Nest Predation in Relation to Forest Fragmentation: A Landscape Perspective. Ecology **73**:794-804.

Aparicio, J., J. Ortego, and P. Cordero. 2006. What should we weigh to estimate heterozygosity, alleles or loci? Molecular Ecology **15**:4659-4665.

Arcese, P. 2003. Individual quality, environment and conservation. Pages 271-296 *in* M. Festa-Bianchet and M. Appolino, editors. Animal Behaviour and Wildlife Conservation. Island Press, Washington D.C.

Ardia, D. R. 2005. Super size me: an experimental test of the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings. Functional Ecology **19**:414-420.

Backström, N., S. Fagerberg, and H. Ellegren. 2008. Genomics of natural bird populations: a gene-based set of reference markers evenly spread across the avian genome. Molecular Ecology **17**:964-980.

Baguette, M. and H. Van Dyck. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecology **22**:1117-1129.

Balkenhol, N., F. Gugerli, S. A. Cushman, L. P. Waits, A. Coulon, J. W. Arntzen, R. Holderegger, H. H. Wagner, P. Arens, P. Campagne, V. H. Dale, A. G. Nicieza, M. J. M. Smulders, E. Tedesco, H. Wang, and T. Wasserman. 2009a. Identifying future research needs in landscape genetics: Where to from here? Landscape Ecology **24**:455-463.

Balkenhol, N. and E. L. Landguth. 2011. Simulation modelling in landscape genetics: On the need to go further. Molecular Ecology **20**:667-670.

Balkenhol, N., L. P. Waits, and R. J. Dezzani. 2009b. Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. Ecography **32**:818-830.

Banbura, J., M. Banbura, A. Kalinski, J. Skwarska, R. Slomczynski, J. Wawrzyniak, and P. Zielinski. 2007. Habitat and year-to-year variation in haernoglobin concentration in nestling blue tits Cyanistes caeruleus. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology **148**:572-577.

Banks, S. C., J. Dubach, K. L. Viggers, and D. B. Lindenmayer. 2010. Adult survival and microsatellite diversity in possums: effects of major histocompatibility complex-

linked microsatellite diversity but not multilocus inbreeding estimators. Oecologia **162**:359–370.

Banks, S. C. and R. Peakall. 2012. Genetic spatial autocorrelation can readily detect sex-biased dispersal. Molecular Ecology **21**:2092-2105.

Banks, S. C., M. P. Piggott, A. J. Stow, and A. C. Taylor. 2007. Sex and sociality in a disconnected world: A review of the impacts of habitat fragmentation on animal social interactions. Canadian Journal of Zoology **85**:1065-1079.

Banks, S. C., S. J. Ward, D. B. Lindenmayer, G. R. Finlayson, S. J. Lawson, and A. C. Taylor. 2005. The effects of habitat fragmentation on the social kin structure and mating system of the agile antechinus, Antechinus agilis. Molecular Ecology **14**:1789-1801.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes. R package.

Bennett, A. F. and J. Q. Radford. 2009. Thresholds, incidence functions and species-specific cues: responses of woodland birds to landscape structure in south-eastern Australia. Pages 161-184 *in* M. A. Villard and B. G. Jonsson, editors. Setting Conservation Targets for Managed Forest Landscapes. Cambridge University Press

Bennett, J. M., R. H. Clarke, J. R. Thomson, and R. Mac Nally. 2014a. Fragmentation, vegetation change and irruptive competitors affect recruitment of woodland birds. Ecography.

Bennett, J. M., R. H. Clarke, J. R. Thomson, and R. Mac Nally. 2014b. Variation in abundance of nectarivorous birds: does a competitive despot interfere with flower tracking? Journal of Animal Ecology:n/a-n/a.

Bennett, J. M., D. G. Nimmo, R. H. Clarke, M. Hall, J. R. Thomson, J. Q. Radford, A. F. Bennett, and R. Mac Nally. 2014c. Resistance and resilience to pressures: Can the abrupt end of extreme drought reverse the collapse of an avifauna? Diversity and Distributions.

Bensch, S., T. Price, and J. Kohn. 1997. Isolation and characterization of microsatellite loci in a *Phylloscopus* warbler. Molecular Ecology **6**:91-92.

Berry, L. 2002. Predation rates of artificial nests in the edge and interior of a southern Victorian forest. Wildlife Research **29**:341-345.

Blackmore, C. J., R. Peakall, and R. Heinsohn. 2011. The absence of sex-biased dispersal in the cooperatively breeding grey-crowned babbler. Journal of Animal Ecology **80**:69-78.

Blair, C., V. H. Jimenez Arcos, F. R. Mendez de la Cruz, and R. W. Murphy. 2013. Landscape genetics of leaf-toed geckos in the tropical dry forest of northern Mexico. PLoS ONE **8**:e57433.

Blair, M. E. and D. J. Melnick. 2012. Scale-dependent effects of a heterogeneous landscape on genetic differentiation in the Central American squirrel monkey (Saimiri oerstedii). PLoS ONE **7**:e43027.

Bojarinova, J. G., E. Lehikoinen, and T. Eeva. 1999. Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. Journal of Avian Biology:437-446.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127-135.

Bosschieter, L. and P. W. Goedhart. 2005. Gap crossing decisions by reed warblers (*Acrocephalus scirpaceus*) in agricultural landscapes. Landscape Ecology **20**:455-468.

Bowcock, A., A. Ruiz-Linares, J. Tomfohrde, E. Minch, J. Kidd, and L. L. Cavalli-Sforza. 1994. High resolution of human evolutionary trees with polymorphic microsatellites. Nature **368**:455-457.

Bradburd, G. S., P. L. Ralph, and G. M. Coop. 2013a. Disentangling the effects of geographic and ecological isolation on genetic differentiation. Evolution **67**:3258-3273.

Bradburd, G. S., P. L. Ralph, and G. M. Coop. 2013b. Disentangling the effects of geographic and ecological isolation on genetic differentiation. Evolution **67**:3258-3273.

Broquet, T., N. Ray, E. Petit, J. M. Fryxell, and F. Burel. 2006. Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). Landscape Ecology **21**:877-889.

Callens, T., P. Galbusera, E. Matthysen, E. Y. Durand, M. Githiru, J. R. Huyghe, and L. Lens. 2011. Genetic signature of population fragmentation varies with mobility in

seven bird species of a fragmented Kenyan cloud forest. Molecular Ecology **20**:1829–1844.

Campbell, T. W. 1995. Avain Hemotology and Cytology. 2nd edition. Iowa State University Press.

Caughley, G. 1994. Directions in Conservation Biology. The Journal of Animal Ecology **63**:215-244.

Chapman, J. R., S. Nakagawa, D. W. Coltman, J. Slate, and B. C. Sheldon. 2009. A quantitative review of heterozygosity-fitness correlations in animal populations. Mol Ecol **18**:2746-2765.

Chen, C., E. Durand, F. Forbes, and O. Francois. 2007. Bayesian clustering algorithms ascertaining spatial population structure: a new computer program and a comparison study. Molecular Ecology Notes **7**:747-756.

Colson, K. E., T. J. Brinkman, D. K. Person, and K. J. Hundertmark. 2012. Fine-scale social and spatial genetic structure in Sitka black-tailed deer. Conservation Genetics:1-11.

Coltman, D. W., J. G. Pilkington, J. A. Smith, and J. M. Pemberton. 1999. Parasite-mediated selection against inbred soay sheep in a free-living island populations. Evolution **53**:1259-1267.

Compton, B. W., K. Mcgarigal, S. A. Cushman, and L. R. Gamble. 2007. A Resistant-Kernel Model of Connectivity for Amphibians that Breed in Vernal Pools. Conservation Biology **21**:788-799.

Cooper, C. B. and J. R. Walters. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. Conservation Biology **16**:471-478.

Cooper, C. B., J. R. Walters, and H. Ford. 2002. Effects of remnant size and connectivity on the response of Brown Treecreepers to habitat fragmentation. Emu **102**:249-256.

Coulon, A. 2010. genhet: an easy-to-use R function to estimate individual heterozygosity. Molecular Ecology Resources **10**:167-169.

Coulon, A., J. F. Cosson, J. M. Angibault, B. Cargnelutti, M. Galan, N. Morellet, E. Petit, S. Aulagnier, and A. J. M. Hewison. 2004. Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. Molecular Ecology **13**:2841-2850.

Coulon, A., G. Guillot, J.-F. Cosson, J. M. A. Angibault, Aulagnier S, B. Cargnelutti, M. Galan, and A. J. M. Hewison 2006. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. Molecular Ecology **15**:1669-1679.

Coulson, T., S. Albon, J. Slate, and J. M. Pemberton. 1999. Microsatellite loci reveal sex-dependent responses to inbreeding and outbreeding in red deer calves. Evolution **53**:1953-1960.

Coulson, T. N., J. M. Pemberton, S. D. Albon, M. Beaumont, T. C. Marshall, J. Slate, F. E. Guinness, and T. H. Cluttonbrock. 1998. Microsatellites reveal heterosis in red deer. Proceedings of the Royal Society of London - Series B: Biological Sciences **265**:489-495.

Crooks, K. R. and M. Sanjayan, editors. 2006. Connectivity conservation: maintaining connections for nature. Cambridge University Press, Cambridge.

Cushman, S. A. and E. L. Landguth. 2010. Spurious correlations and inference in landscape genetics. Molecular Ecology **19**:3592-3602.

Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: Testing multiple hypotheses with causal modeling. American Naturalist **168**:486-499.

Cushman, S. A., K. S. McKelvey, and M. K. Schwartz. 2009. Use of empirically derived source-destination models to map regional conservation corridors. Conservation Biology **23**:368-376.

Cushman, S. A., M. G. Raphael , L. F. Ruggiero, A. J. Shirk, T. Wasserman, and E. C. O'Doherty. 2011. Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. Landscape Ecology **26**:1137-1149.

Cushman, S. A., T. N. Wasserman, E. L. Landguth, and A. J. Shirk. 2013. Re-Evaluating Causal Modeling with Mantel Tests in Landscape Genetics. Diversity **5**:51-72.

Czembor, C. A., W. K. Morris, B. A. Wintle, and P. A. Vesk. 2011. Quantifying variance components in ecological models based on expert opinion. Journal of Applied Ecology **48**:736–745.

Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos **92**:344-356.

Dawson, D. A., O. Hanotte, C. Greig, I. R. K. Stewart, and T. Burke. 2000. Polymorphic microsatellites in the blue tit *Parus caeruleus* and their cross-species utility in 20 songbird families. Molecular Ecology **9**:1941-1944.

Dawson, R. D. and G. R. Bortolotti. 1997. Are avian hematocrits indicative of condition? American kestrels as a model. Journal of Wildlife Management **61**:1297-1306.

Debus, S. J. S. and H. A. Ford. 2012. Responses of Eastern Yellow Robins *Eopsaltria australis* to translocation into vegetation remnants in a fragmented landscape. . Pacific conservation biology **18**:194-202.

Department of Sustainability and Environment. 2008. NV2005_QUAL. Department of Sustainability and Environment, East Melbourne.

Dijkstra, E. W. 1959. A note on two problems in connexion with graphs. Numerische Mathematik **1**:269-271.

Dixon, P. 2003. VEGAN, a package of R functions for community ecology. Journal of Vegetation Science **14**:927-930.

Doerr, E. D. 2005. Characterization of microsatellite loci in the brown treecreeper (*Climacteris picumnus*) and cross-species amplification in the white-throated treecreeper (*Cormobates leucophaeus*). Molecular Ecology Notes **5**:654-656.

Doerr, E. D., V. A. J. Doerr, M. Davies, and H. McGinness. 2014. Does structural connectivity facilitate movement of native species in Australia's fragmented landscapes?: a systematic review protocol. Environmental Evidence **3**.

Doerr, V. A. J., E. D. Doerr, and M. J. Davies. 2011. Dispersal behaviour of Brown Treecreepers predicts functional connectivity for several other woodland birds. Emu **111**:71-83.

Double, M. C., D. Dawson, T. Burke, and A. Cockburn. 1997. Finding the fathers in the least faithful bird: A microsatellite-based genotyping system for the superb fairy-wren Malurus cyaneus. Molecular Ecology **6**:691-693.

Dowling, D. K., G. J. Adcock, and R. A. Mulder. 2003. Novel polymorphic microsatellite markers for paternity analysis in the red-capped robin (*Petroica goodenovii*: Aves). Molecular Ecology Notes **3**:517-519.

Driezen, K., F. Adriaensen, C. Rondinini, C. P. Doncaster, and E. Matthysen. 2007. Evaluating least-cost model predictions with empirical dispersal data: A case-study using radiotracking data of hedgehogs (Erinaceus europaeus). Ecological Modelling **209**:314-322.

DSE. 1990-1999. TREE25 Raster Dataset. Department of Sustainability and Environment, East Melbourne.

DSE. 2007. NV1750_EVC Vector Dataset. Department of Sustainability and Environment, East Melbourne.

Dudaniec, R. Y., S. Kleindorfer, and B. Fessl. 2006. Effects of the introduced ectoparasite Philornis downsi on haemoglobin level and nestling survival in Darwin's Small Ground Finch (Geospiza fuliginosa). Austral Ecology **31**:88-94.

Eklom, K. and A. Lill. 2006. Development pattern of blood oxygen carrying capacity in rainbow bee-eater nestlings. Australian Journal of Zoology **54**:1-7.

Environment Conservation Council. 1997. Box-ironbark forests and woodlands investigation: resources and issues report. Environment Conservation Council, East Melbourne, Australia.

Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology **44**:714-724.

ESRI. 1999-2008. ArcGIS Desktop: Release 9.3. Environmental Systems Research Institute., Redlands, CA.

Ewers, R. M. and R. K. Didham. 2005. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews **81**:117.

Excoffier, L. and H. E. L. Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. . Molecular Ecology Resources. **10**:564-567.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation **100**:65-74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics **34**:487-515.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology **21**:1003-1015.

Fair, J., S. Whitaker, and B. Pearson. 2007. Sources of variation in haematocrit in birds. Ibis **149**:535-552.

Ferrier, S., G. Manion, J. Elith, and K. Richardson. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and Distributions **13**:252-264.

Ferwerda, F. 2003. Assessing the importance of remnant native vegetation for maintaining biodiversity in rural landscapes using geospatial analysis. RMIT University.

Ford, H. A. 1985. Nectarivory and pollination by birds in southern Australia and Europe. Oikos **44**:127-131.

Ford, H. A. 2011a. The causes of decline of birds of eucalypt woodlands: advances in our knowledge over the last 10 years. Emu **111**:1-9.

Ford, H. A. 2011b. Twinkling lights or turning down the dimmer switch?: Are there two patterns of extinction debt in fragmented landscapes? Pacific conservation biology **17**:303.

Ford, H. A., G. W. Barrett, D. A. Saunders, and H. F. Recher. 2001. Why have birds in the woodlands of southern Australia declined? Biological Conservation **97**:71-88.

Frankham, R. 2005. Genetics and extinction. Biological Conservation **126**:131-140.

Frankham, R. and K. Ralls. 1998. Conservation biology - inbreeding leads to extinction. Nature **392**:441-442.

Garcia-Navas, V., J. Ortego, and J. J. Sanz. 2009. Heterozygosity-based assortative mating in blue tits (Cyanistes caeruleus): implications for the evolution of mate choice. Proceedings of the Royal Society B: Biological Sciences **276**:2931-2940.

Garrard, G. E., M. A. McCarthy, P. A. Vesk, J. Q. Radford, and A. F. Bennett. 2012. A predictive model of avian natal dispersal distance provides prior information for investigating response to landscape change. J Anim Ecol **81**:14-23.

Gorrod, E. J. and D. A. Keith. 2009. Observer variation in field assessments of vegetation condition: Implications for biodiversity conservation. Ecological Management and Restoration **10**:31-40.

Goslee, S. and D. L. Urban. 2007. The ecodist Package for Dissimilarity-based Analysis. Journal of Statistical Software **22**:1-19.

Goudet, J. 2005. hierfstat, a package for r to compute and test hierarchical F-statistics. Molecular Ecology Notes **5**:184-186.

Graves, T. A. 2012. Spatial ecology of grizzly bears in northwestern Montana and estimating resistance to gene flow. Northern Arizona University.

Graves, T. A., P. Beier, and J. A. Royle. 2013. Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. Mol Ecol **22**:3888-3903.

Green, A. J. 2001. Mass/Length Residuals: Measures of Body Condition or Generators of Spurious Results? Ecology **82**:1473-1483.

Grey, M. J., M. F. Clarke, and R. H. Loyn. 1997. Initial changes in the avian communities of remnant eucalypt woodlands following a reduction in the abundance of noisy miners, Manorina melanocephala. Wildlife Research **24**:631-648.

Griffith, S. C., I. R. K. Stewart, D. A. Dawson, I. P. F. Owens, and T. Burke. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an 'island effect'? Biological Journal of the Linnean Society **68**:303-316.

Hanotte, O., C. Zanon, A. Pugh, C. Greig, A. Dixon, and T. Burke. 1994. Isolation and characterization of microsatellite loci in a passerine bird: The reed bunting *Emberiza schoeniclus*. Molecular Ecology **3**:529-530.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos **87**:209-219.

Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. American Naturalist **147**:527-541.

Hanski, I. and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature **404**:755-758.

Hanski, I. and O. Ovaskainen. 2002. Extinction debt at extinction threshold. Conservation Biology **16**:666-673.

Hansson, B., S. Bensch, D. Hasselquist, and M. Akesson. 2001. Microsatellite diversity predicts recruitment of sibling great reed warblers. Proceedings of the Royal Society of London Series B-Biological Sciences **268**:1287–1291.

Harrisson, K. A., A. Pavlova, J. N. Amos, J. Q. Radford, and P. Sunnucks. 2014. Does reduced mobility through fragmented landscapes explain patch extinction patterns for three honeyeaters? J Anim Ecol **83**:616-627.

Harrisson, K. A., A. Pavlova, J. N. Amos, N. Takeuchi, A. Lill, J. Q. Radford, and P. Sunnucks. 2012. Fine-scale effects of habitat loss and fragmentation despite large-scale gene flow for some regionally declining woodland bird species. Landscape Ecology **27**:813-827.

Harrisson, K. A., A. Pavlova, J. N. Amos, N. Takeuchi, A. Lill, J. Q. Radford, and P. Sunnucks. 2013. Disrupted fine-scale population processes in fragmented

landscapes despite large-scale genetic connectivity for a widespread and common cooperative breeder: the superb fairy-wren (Malurus cyaneus). J Anim Ecol.

Higgins, P. J. and J. M. Peter, editors. 2002. Handbook of Australian, New Zealand and Antarctic Birds. Volume 6: Pardalotes to Shrike-thrushes. Oxford University Press Melbourne.

Higgins, P. J., J. M. Peter, and S. J. Cowling, editors. 2006. Handbook of Australian, New Zealand and Antarctic Birds. Volume 7: Boatbill to Starlings. Oxford University Press Melbourne.

Higgins, P. J., J. M. Peter, and W. K. Steele, editors. 2001. Handbook of Australian, New Zealand and Antarctic Birds. Volume 5: Tyrant-flycatchers to Chats. Oxford University Press Melbourne.

Hilden, J. 1991. The area under the ROC curve and its competitors. Medical Decision Making **11**:95-101.

Hilty, J. A., W. Z. Lidicker, and A. M. Merenlender. 2006. Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island Press, Washington D.C.

Holderegger, R. and H. H. Wagner. 2008. Landscape genetics. Bioscience **58**:199-207.

Hõrak, P., S. Jenni-Eiermann, I. Ots, and L. Tegelmann. 1998. Health and reproduction: The sex-specific clinical profile of great tits (Parus major) in relation to breeding. Canadian Journal of Zoology **76**:2235-2244.

Huhta, E., T. Aho, A. Jäntti, P. Suorsa, M. Kuitunen, A. Nikula, and H. Hakkarainen. 2004. Forest Fragmentation Increases Nest Predation in the Eurasian Treecreeper. Conservation Biology **18**:148-155.

Jakobsson, M. and N. A. Rosenberg. 2007. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics **23**:1801-1806.

James, P. M. A., D. W. Coltman, B. W. Murray, R. C. Hamelin, and F. A. H. Sperling. 2011. Spatial Genetic Structure of a Symbiotic Beetle-Fungal System: Toward Multi-Taxa Integrated Landscape Genetics. PLoS ONE **6**:e25359.

Jaquiéry, J., T. Broquet, A. H. Hirzel, J. Yearsley, and N. Perrin. 2011. Inferring landscape effects on dispersal from genetic distances: how far can we go? Molecular Ecology **20**:692-705.

Jeffery, K. J., L. F. Keller, P. Arcese, and M. W. Bruford. 2001. The development of microsatellite loci in the song sparrow, *Melospiza melodia* (Aves) and genotyping errors associated with good quality DNA. Molecular Ecology Notes **1**:11-13.

Jeffreys, H. 1961. Theory of probability. Oxford University Press, Oxford.

Jeness, J. Undated. Export to Circuitscape Tool for ArcGIS 9.x Jenness Enterprises, Flagstaff.

Jin, L., K. Munro, S. Tan, J. Hoffman, and W. Amos. 2006. Polymorphic microsatellite DNA markers for the grey fantail, *Rhipidura albiscapa*. Molecular Ecology Notes **6**:75-76.

Johnstone, C., A. Lill, and R. Reina. 2011. Does habitat fragmentation cause stress in the agile antechinus? A haematological approach. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology:1-17.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology **16**:1099-1106.

Kilgas, P., V. Tilgar, and R. Mand. 2006. Hematological health state indices predict local survival in a small passerine bird, the great tit (Parus major). Physiological and Biochemical Zoology **79**:565-572.

Koen, E. L., G. C.J, P. J. Wilson, and J. Bowman. 2010a. The Effect of Map Boundary on Estimates of Landscape Resistance to Animal Movement. PLoS ONE **5**:e11785.

Koen, E. L., C. J. Garroway, P. J. Wilson, and J. Bowman. 2010b. The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE **5**:e11785.

Lada, H., R. Mac Nally, and A. C. Taylor. 2008a. Distinguishing past from present gene flow along and across a river: The case of the carnivorous marsupial (*Antechinus flavipes*) on southern Australian floodplains. Conservation Genetics **9**:569-580.

Lada, H., J. R. Thomson, R. Mac Nally, and A. C. Taylor. 2008b. Impacts of massive landscape change on a carnivorous marsupial in south-eastern Australia: inferences from landscape genetics analysis. Journal of Applied Ecology **45**:1732-1741.

Laiolo, P. and J. L. Tella. 2005. Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's lark. Journal of Applied Ecology **42**:1183-1193.

Landguth, E., J. Glassy, S. Cushman, M. Jacobi, T. Julian, B. Hand, and A. Warren. 2013 CDPOP User Manual Version: 1.2.19

Landguth, E., B. Hand, J. Glassy, S. Cushmann, and M. Sawaya. 2012a. UNICOR: a species connectivity and corridor network simulator. Ecography.

Landguth, E. L. and S. A. Cushman. 2010. CDPOP: A spatially explicit cost distance population genetics program. Molecular Ecology Resources **10**:156-161.

Landguth, E. L., S. A. Cushman, M. A. Murphy, and G. Luikart. 2010a. Relationships between migration rates and landscape resistance assessed using individual-based simulations. Molecular Ecology Resources **10**:854-862.

Landguth, E. L., S. A. Cushman, M. K. Schwartz, K. S. McKelvey, M. Murphy, and G. Luikart. 2010b. Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology **19**:4179-4191.

Landguth, E. L., B. C. Fedy, S. J. Oyler-McCance, A. L. Garey, S. L. Emel, M. Mumma, H. H. Wagner, M.-J. Fortin, and S. A. Cushman. 2012b. Effects of sample size, number of markers, and allelic richness on the detection of spatial genetic pattern. Molecular Ecology Resources **12**:276-284.

Latta, S. C. and J. Faaborg. 2002. Demographic and Population Responses of Cape May Warblers Wintering in Multiple Habitats. Ecology **83**:2502-2515.

Leblanc, M. J., P. Tregoning, G. Ramillien, S. O. Tweed, and A. Fakes. 2009. Basin-scale, integrated observations of the early 21st century multiyear drought in southeast Australia. WATER RESOURCES RESEARCH **45**:W04408.

Legendre, P. and M.-J. Fortin. 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. Molecular Ecology Resources **10**:831-844.

Legendre, P., F.-J. Lapointe, and P. Casgrain. 1994. Modeling brain evolution from behavior: a permutational regression approach. Evolution:1487-1499.

Legendre, P. and M. Troussellier. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnology & Oceanography **33**:1055-1067.

Li, S. H., Y. J. Huang, and J. L. Brown. 1997. Isolation of tetranucleotide microsatellites from the Mexican jay *Aphelocoma ultramarina*. Molecular Ecology **6**:499-501.

Lindenmayer, D. and J. Fischer. 2006. Habitat fragmentation and landscape change an ecological and conservation synthesis. CSIRO Publishing, Collingwood.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, L. Fahrig, J. Fischer, J. Franklin, Y. Haila, M. Hunter, P. Gibbons, S. Lake, G. Luck, C. MacGregor, S. McIntyre, R. M. Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Simberloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J. Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters **11**:78-91.

Lindenmayer, D. and G. Luck. 2005. Synthesis: thresholds in conservation and management. Biological Conservation **124**:351-354.

Lindenmayer, D. B. and J. Fischer. 2007. Tackling the habitat fragmentation panchreston. Trends in Ecology and Evolution **22**:127-132.

Linkie, M., G. Chapron, D. J. Martyr, J. Holden, and N. Leader-Williams. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. Journal of Applied Ecology **43**:576-586.

Liu, C., M. White, G. Newell, and P. Griffioen. 2012. Species distribution modelling for conservation planning in Victoria, Australia. Ecological Modelling.

Loehle, C. and B.-L. Li. 1996. Habitat destruction and the extinction debt revisited. Ecological Applications **6**:784-789.

Lowe, W. H. and F. W. Allendorf. 2010. What can genetics tell us about population connectivity? Molecular Ecology **19**:3038-3051.

Lunn, D. J., N. Best, and J. C. Whittaker. 2009. Generic reversible jump MCMC using graphical models. Statistics and Computing **19**.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS- a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing **10**:325-337.

Mac Nally, R. 1990. The roles of floristics and physionomy in avian community composition. Australian Journal of Ecology **15**.

Mac Nally, R. and A. F. Bennett. 1997. Species-specific predictions of the impact of habitat fragmentation: Local extinction of birds in the box-ironbark forests of central Victoria, Australia. Biological Conservation **82**:147-155.

Mac Nally, R., A. F. Bennett, and G. Horrocks. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat

fragmentation on birds in the box-ironbark forests of central Victoria, Australia. Biological Conservation **95**:7-29.

Mac Nally, R., A. F. Bennett, J. R. Thomson, J. Q. Radford, G. Unmack, G. Horrocks, and P. A. Vesk. 2009. Collapse of an avifauna: Climate change appears to exacerbate habitat loss and degradation. Diversity and Distributions **15**:720-730.

Manel, S. and R. Holderegger. 2013. Ten years of landscape genetics. Trends Ecol Evol **28**:614-621.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: Combining landscape ecology and population genetics. Trends in Ecology & Evolution **18**:189-197.

Maron, M., A. Main, M. Bowen, A. Howes, J. Kath, C. Pillette, and C. A. McAlpine. 2011. Relative influence of habitat modification and interspecific competition on woodland bird assemblages in eastern Australia. Emu **111**:40-51.

Martin, T. G. and H. P. Possingham. 2005. Predicting the impact of livestock grazing on birds using foraging height data. Journal of Applied Ecology **42**:400-408.

Martinez, J. G., J. J. Soler, M. Soler, A. P. Miller, and T. Burke. 1999. Comparative population structure and gene flow of a brood parasite, the great spotted cuckoo (*Clamator glandarius*), and its primary host, the magpie (*Pica pica*). Evolution **53**:269-278.

Mazerolle, D. F. and K. A. Hobson. 2002. Physiological ramifications of habitat selection in territorial male ovenbirds: consequences of landscape fragmentation. Oecologia **130**:356-363.

McGarigal, K. 2014. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

McIntire, E. J. B. and A. Fajardo. 2009. Beyond description: The active and effective way to infer processes from spatial patterns. Ecology **90**:46-56.

McRae, B. H. 2006. Isolation by resistance. Evolution **60**:1551-1561.

McRae, B. H. and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences of the United States of America **104**:19885-19890.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolotion and conservation. Ecology **89**:2712-2724.

McRae, B. H. and V. B. Shah. 2009. Circuitscape user's guide. The University of California, Santa Barbara.

Merriam, G. 1984. Connectivity: A fundamental ecological characteristic of landscape pattern.*in* Proceeding of the 1st international seminar on methodology in landscape ecological research and planning. . Roskilde University., Roskilde, Denmark.

Mönkkönen, M. and P. Reunanen. 1999. On Critical Thresholds in Landscape Connectivity: A Management Perspective. Oikos **84**:302-305.

Moore, J. A., D. A. Tallmon, J. Nielsen, and S. Pyare. 2011. Effects of the landscape on boreal toad gene flow: does the pattern-process relationship hold true across distinct landscapes at the northern range margin? Mol Ecol **20**:4858-4869.

Morales, J. M. and S. P. Ellner. 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. Ecology **83**:2240-2247.

Mulder, R. A. 1995. Natal and breeding dispersal in a co-operative, extra-group-mating bird. Journal of Avian Biology **26**:234-240.

Mulder, R. A., P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen, and M. J. Howell. 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. Proceedings: Biological Sciences:223-229.

Munshi-South, J. 2012. Urban landscape genetics: canopy cover predicts gene flow between white-footed mouse (Peromyscus leucopus) populations in New York City. Mol Ecol **21**:1360-1378.

Myers, S. A., M. G. Gardner, S. Donnellan, and S. Kleindorfer. 2009. New Holland honeyeater (*Phylidonyris novaehollandiae*) microsatellites: isolation and characterization of 15 novel markers using an enrichment method. Molecular Ecology Resources **9**:1052-1054.

Norte, A., J. Ramos, J. Sousa, and B. Sheldon. 2009a. Variation of adult Great Tit *Parus major* body condition and blood parameters in relation to sex, age, year and season. Journal of Ornithology **150**:651-660.

Norte, A. C., J. A. Ramos, H. L. Sampaio, J. P. Sousa, and B. C. Sheldon. 2010. Physiological Condition and Breeding Performance of the Great TIT. The Condor **112**:79-86.

Norte, C. A., B. C. Sheldon, J. P. Sousa, and J. A. Ramos. 2009b. Environmental and genetic variation in body condition and blood profile of great tit Parus major nestlings. Journal of Avian Biology **40**:157-165.

Noske, R. 1991. A Demographic Comparison of Cooperatively Breeding and Non-cooperative Treecreepers (Climacteridae). Emu **91**:73-86.

Oksanen, J., Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, and W. H. 2012. vegan: Community Ecology Package R package version 2.0-3.

Olsen, P., M. Weston, C. Tzaros, and A. Silcocks. 2005. The State of Australia's Birds 2005: Woodlands and Birds. Wingspan **15**.

Ots, I., A. Murumagi, and P. Horak. 1998. Haematological health state indices of reproducing Great Tits: methodology and sources of natural variation. Functional Ecology **12**:700-707.

Oyler-McCance, S. J., B. C. Fedy, and E. L. Landguth. 2012. Sample design effects in landscape genetics. Conservation Genetics **14**:275-285.

Painter, J., R. H. Crozier, Y. C. Crozier, and M. F. Clarke. 1997. Characterization of microsatellite loci for a co-operatively breeding honeyeater. Molecular Ecology **6**:1103-1105.

Palstra, F. P. and D. E. Ruzzante. 2008. Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence? Molecular Ecology **17**:3428-3447.

Parkes, D., G. Newell, and D. Cheal. 2003. Assessing the quality of native vegetation: The 'habitat hectares' approach. Ecological Management and Restoration **4**.

Pavlova, A., J. N. Amos, M. I. Goretskaia, I. R. Beme, K. Buchanan, N. Takeuchi, J. Q. Radford, and P. Sunnucks. 2012. Genes and song: genetic and social connections in fragmented habitat in a woodland bird with limited dispersal. Ecology.

Pavlova, A., J. N. Amos, L. Joseph, K. Loynes, J. J. Austin, J. S. Keogh, G. N. Stone, J. A. Nicholls, and P. Sunnucks. 2013. Perched at the mito-nuclear crossroads: divergent mitochondrial lineages correlate with environment in the face of ongoing nuclear gene flow in an Australian bird. Evolution **67**:3412-3428.

Payne, R. W., D. A. Murray, S. A. Harding, D. B. Baird, and D. M. Soutar. 2007. GenStat for windows. VSN International Ltd., Hemel Hempstead, UK.

Peakall, R. and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes **6**:288-295.

Piertney, S. B., M. Marquiss, and R. Summers. 1998. Characterization of tetranucleotide microsatellite markers in the Scottish crossbill (*Loxia scotica*). Molecular Ecology **7**:1261-1263.

Pinto, N. and T. H. Keitt. 2009. Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landscape Ecology **24**:253-266.

Piper, S. D. and C. P. Catterall. 2003. A particular case and a general pattern: hyperaggressive behaviour by one species may mediate avifaunal decreases in fragmented Australian forests. Oikos **101**:602-614.

Porlier, M., M. Belisle, and D. Garant. 2009. Non-random distribution of individual genetic diversity along an environmental gradient. Philosophical Transactions of the Royal Society B: Biological Sciences **364**:1543-1554.

Primmer, C. R., A. P. Moller, and H. Ellegren. 1995. Resolving genetic relationships with microsatellite markers: A parentage testing system for the swallow *Hirundo rustica*. Molecular Ecology **4**:493-498.

Primmer, C. R., A. P. Moller, and H. Ellegren. 1996. A wide-range survey of cross-species microsatellite amplification in birds. Molecular Ecology **5**:365-378.

Qian, S. S., R. S. King, C. J. Richardson, and 2003. Two statistical methods for the detection of environmental thresholds. Ecological Modelling : **166**:87-97.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Radford, J. Q. and A. F. Bennett. 2007. The relative importance of landscape properties for woodland birds in agricultural environments. Journal of Applied Ecology **44**:737-747.

Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. Biological Conservation **124**:317-337.

Reilly, P. 1968. A flame robin trap. Australian Bird bander 82-83.

Robertson, O. J. and J. Q. Radford. 2009. Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecology **34**:435–446.

Robinson, D. and B. J. Traill. 1996. Conserving woodland birds in the wheat and sheep belts of southern Australia. Royal Australasian Orinithological Union, Melbounre.

Rogers, K., A. Rogers, D. Rogers, B. Lane, and B. Male. 1986. Bander's aid: Aguide to aging and sexing bush birds. A. Rogers; St. Andrews, Victoria.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia **67**:213-217.

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

Rousset, F. 2000. Genetic differentiation between individuals. Journal of Evolutionary Biology **13**:58-62.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature **392**:491-494.

Sackett, L. C., T. B. Cross, R. T. Jones, W. C. Johnson, K. Ballare, C. Ray, S. K. Collinge, and A. P. Martin. 2012. Connectivity of prairie dog colonies in an altered landscape: inferences from analysis of microsatellite DNA variation. Conservation Genetics:1-12.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological Consequences of Ecosystem Fragmentation: A Review. Conservation Biology **5**:18-32.

Schmuki, C., C. Vorburger, D. Runciman, S. MacEachern, and P. Sunnucks. 2006. When log-dwellers meet loggers: Impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern Australia. Molecular Ecology **15**:1481-1492.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology **86**:155-163.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology **90**:3222-3232.

Seddon, N., W. Amos, R. A. Mulder, and J. A. Tobias. 2004. Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird. Proceedings of the Royal Society of London Series B-Biological Sciences **271**:1823-1829.

Seewagen, C. L. 2008. An evaluation of condition indices and predictive models for noninvasive estimates of lipid mass of migrating Common Yellowthroats, Ovenbirds, and Swainson's Thrushes. Journal of Field Ornithology **79**:80-86.

Segelbacher, G., S. A. Cushman, B. K. Epperson, M. J. Fortin, O. Francois, O. J. Hardy, R. Holderegger, P. Taberlet, L. P. Waits, and S. Manel. 2010. Applications of landscape genetics in conservation biology: concepts and challenges. Conservation Genetics:1-11.

Segelbacher, G., S. Manel, and J. Tomiuk. 2008. Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). Molecular Ecology **17**:2356-2367.

Shanahan, D. F. and H. P. Possingham. 2009. Predicting avian patch occupancy in a fragmented landscape: do we know more than we think? Journal of Applied Ecology **46**:1026-1035.

Shanahan, D. F., H. P. Possingham, and C. Riginos. 2010. Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. Landscape Ecology **26**:137-148.

Shirk, A. J., D. O. Wallin, S. A. Cushman, C. G. Rice, and K. I. Warheit. 2010. Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology **19**:3603-3619.

Short Bull, R. A., S. A. Cushman, R. Mace, T. Chilton, K. C. Kendall, E. L. Landguth, M. K. Schwartz, K. McKelvey, F. W. Allendorf, and G. Luikart. 2011. Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Molecular Ecology **20**:1092–1107.

Siegel, S. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

Simmons, P. and A. Lill. 2006. Development of parameters influencing blood oxygen carrying capacity in the welcome swallow and fairy martin. Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology **143**:459-468.

Smouse, P. E. and R. Peakall. 1999. Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity (Edinb) **82 (Pt 5)**:561-573.

Spear, S. F., N. Balkenhol, M.-J. Fortin, B. H. McRae, and K. I. M. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology **19**:3576-3591.

Spear, S. F., S. A. Cushman, and B. McRae. 2014. Resistance Surface Modeling in Landscape Genetics. Page 350 *in* N. Balkenhol, S. Cushman, A. Storfer, and L. Waits, editors. Landscape Genetics: Concepts, Methods, Applications. Wiley-Blackwell.

Stevens, V. M., C. Verkenne, S. Vandewoestijne, R. A. Wesselingh, and M. Baguette. 2006. Gene flow and functional connectivity in the natterjack toad. Molecular Ecology **15**:2333-2344.

Stevenson, R. D. and W. A. Woods. 2006. Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology **46**:1169-1190.

Storfer, A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L. P. Waits. 2007. Putting the 'landscape' in landscape genetics. Heredity **98**:128-142.

Stow, A. J., P. Sunnucks, D. A. Briscoe, and M. G. Gardner. 2001. The impact of habitat fragmentation on dispersal of Cunningham's skink (Egernia cunninghami): Evidence from allelic and genotypic analyses of microsatellites. Molecular Ecology **10**:867-878.

Strong, A. M. and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology **69**:883-895.

Sunnucks, P. 2000. Efficient genetic markers for population biology. Trends in Ecology and Evolution **15**:199-203.

Sunnucks, P. 2011. Towards modelling persistence of woodland birds: the role of genetics. Emu **111**:19.

Suorsa, P., E. Huhta, A. Nikula, M. Nikinmaa, A. Jantti, H. Helle, and H. Hakkarainen. 2003a. Forest management is associated with physiological stress in an old-growth forest passerine. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:963-969.

Suorsa, P., H. Helle, E. Huhta, A. Jantti, A. Nikula, and H. Hakkarainen. 2003b. Forest fragmentation is associated with primary brood sex ratio in the treecreeper (Certhia familiaris). Proceedings of the Royal Society B: Biological Sciences **270**:2215-2222.

Szabo, J. K., P. A. Vesk, P. W. J. Baxter, and H. P. Possingham. 2011. Paying the extinction debt: woodland birds in the Mount Lofty Ranges, South Australia. Emu **111**:59-70.

Taylor, P., L. Fahrig, and K. A. With. 2006. Landscape connectivity: back to the basics *in* K. Crooks and M. A. Sanjayan, editors. Connectivity Conservation. Cambridge University Press, Cambridge.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos **68**:571-573.

Tellería, J. L., E. Virgós, R. Carbonell, J. Pérez-Tris, and T. Santos. 2001. Behavioural responses to changing landscapes: Flock structure and anti-predator strategies of tits wintering in fragmented forests. Oikos **95**:253-264.

Theobald, D. M. 2006. Exploring the functional connectivity of landscapes using landscape networks *in* K. Crooks and M. A. Sanjayan, editors. Connectivity Conservation. Cambridge University Press Cambridge.

Thomassen, H. A., Z. A. Cheviron, A. H. Freedman, R. J. Harrigan, R. K. Wayne, and T. B. Smith. 2010. Spatial modelling and landscape-level approaches for visualizing intra-specific variation. Molecular Ecology **19**:3532-3548.

Thomson, J. R., R. Mac Nally, E. Fleishman, and G. Horrocks. 2007. Predicting bird species distributions in reconstructed landscapes. Conservation Biology **21**:752-766.

Toms, J. D. and M. L. Lesperance. 2003. Piecewise regression: A tool for idnentifying ecological thresholds. Ecology **84**:2034-2041.

Trumbo, D. R., S. F. Spear, J. Baumsteiger, and A. Storfer. 2013. Rangewide landscape genetics of an endemic Pacific northwestern salamander. Mol Ecol **22**:1250-1266.

Turcotte, Y. and A. Desrochers. 2008. Forest fragmentation and body condition in wintering black-capped chickadees. Canadian Journal of Zoology **86**:572-581.

Van Houtan, K. S., S. L. Pimm, J. M. Halley, R. O. Bierregaard Jr, and T. E. Lovejoy. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters **10**:219-229.

Vesk, P. and R. Mac Nally. 2006. The clock is ticking - Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. Agriculture Ecosystems and Environment **112**:356-366.

Unfried, T. M., L. Hauser, and J. M. Marzluff. 2012. Effects of urbanization on Song Sparrow (*Melospiza melodia*) population connectivity. Conservation Genetics **14**:41-53.

Walker, R., A. Novaro, and L. Branch. 2007. Functional connectivity defined through cost-distance and genetic analyses: a case study for the rock-dwelling mountain vizcacha (*Lagidium viscacia*) in Patagonia, Argentina. Landscape Ecology **22**:1303-1314.

Walpole, A. A., J. Bowman, D. L. Murray, and P. J. Wilson. 2012. Functional connectivity of lynx at their southern range periphery in Ontario, Canada. Landscape Ecology **27**:761-773.

Wasserman, T. N., S. A. Cushman, M. K. Schwartz, and D. O. Wallin. 2010. Spatial scaling and multi-model inference in landscape genetics: Martes americana in northern Idaho. Landscape Ecology **25**:1601-1612.

Wasserman, T. N., S. A. Cushman, A. S. Shirk, E. L. Landguth, and J. S. Littell. 2011. Simulating the effects of climate change on population connectivity of American marten (Martes americana) in the northern Rocky Mountains, USA. Landscape Ecology.

Watson, D. M. 2011. A productivity-based explanation for woodland bird declines: poorer soils yield less food. Emu **111**:10-18.

Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2004. Reproductive promiscuity in the splendid fairy-wren: effects of group size and auxiliary reproduction. Behavioral Ecology **15**:907-915.

With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos **78**:151-169.

World Resources Institute. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. . World Resources Institute, Washington, DC.

Wright, S. 1943. Isolation by distance. Genetics **38**:114-138.

Xing, J., W. S. Watkins, A. Shlien, E. Walker, C. D. Huff, D. J. Witherspoon, Y. Zhang, T. S. Simonson, R. B. Weiss, J. D. Schiffman, D. Malkin, S. R. Woodward, and L. B. Jorde. 2010. Toward a more uniform sampling of human genetic diversity: A

survey of worldwide populations by high-density genotyping. Genomics **96**:199-210.

Yates, C. J. and R. J. Hobbs. 1997. Temperate eucalypt woodlands: A review of their status, processes threatening their persistence and techniques for restoration. Australian Journal of Botany **45**:949-973.

Zanette, L., P. Doyle, and S. M. Trémont. 2000. Food shortage in small fragments: Evidence from an area-sensitive passerine. Ecology **81**:1654-1666.

Brown Treecreeper (*Climacteris picumnus*)

APPENDICES

Appendix A. Classification of species response in relation to landscape treecover

Methods

We used data from Radford et al. (2007) to identify 'decliner' and 'tolerant' bird species. Species in which landscape-level incidence decreased disproportionately to landscape-level tree cover were classified as 'decliner' species and were identified by a positive relationship between incidence and tree cover. Species in which landscape-level incidence was proportionate to, or increased disproportionately to, landscape-level tree cover were classified as 'tolerant' species and were identified by a null or negative relationship between incidence and tree cover.

There were 10 survey sites in each landscape, distributed within remnant tree cover. Each site was surveyed four times over the course of 12 months. Species incidence per landscape was therefore a score out of 40. The incidence of 58 species in each of the 24 landscapes (Radford and Bennett 2007) was modelled as a function of landscape-level tree cover (TREE). For each species, seven models were fitted using least-squares regression in Genstat V.10 (Payne et al. 2007). We fitted the null model (intercept only, zero slope), four 'continuous' models (linear, logarithmic, quadratic and power) and two 'threshold' models (piecewise and change point). Threshold models separate the response variable into two relatively homogeneous groups either side of a threshold value in the environmental gradient (tree cover in this case). In piecewise regression, the slope of a regression fitted independently to the groups either side of the threshold may vary, whereas in change point analysis the slope of the groups either side of the threshold is always zero (i.e. the groups are characterised by a different mean and deviance).

When the response data are divided into two groups, the sum of the deviance for the two sub-groups is always less than or equal to the deviance of the entire data (Qian et al. 2003). Therefore, each possible threshold (i.e. value in the range of the environmental variable) is associated with a deviance reduction. To identify the threshold in landscape-level tree cover that maximises the deviance reduction for the piecewise (T_{pw}) and change point (T_{cp}) models, sequential values of tree cover (from 0 to 60% tree cover) were fitted and the value with lowest residual deviance identified as the threshold.

To reduce heteroscedasticity, species incidence was first weighted by 1 / (variance + 0.5), where variance was calculated for sequential groups of four landscapes (ordered by increasing tree cover). The best model for each species among the seven candidate models was selected using AIC_c. The models fitted were:

- Null (intercept only): $y = mean(y)$
- Linear: $y = \beta_0 + \beta_1 * TREE$
- Logarithmic: $y = \beta_0 + \beta_1 * Log_{10}(TREE)$
- Quadratic: $y = \beta_0 + \beta_1 * TREE + \beta_2 * TREE^2$
- Power: $y = \beta_0 + \beta_1 * TREE^{\beta 2}$
- Piecewise: $y = \beta_0 + \beta_1 * TREE$ where $TREE < T_{pw}$; $y = \beta_0 + \beta_1 * TREE + \beta_2 * (TREE - T_{pw})$ where $TREE > T_{pw}$ (Toms and Lesperance 2003)
- Binomial change point: $y = \beta_0 + \beta_1 * T_{term}$; where $TREE < T_{cp}$, $T_{term} = 0$; where $TREE > T_{cp}$, $T_{term} = 1$ (Siegel 1988)

Surveys were conducted only within remnant tree cover in each landscape (Radford et al. 2005). This means that the null model represents a proportionate decline in number of birds with landscape tree cover; that is, incidence in a patch of suitable habitat is not related to the overall proportion of tree cover in that landscape. Thus, species in which the null model was selected as the best fit were identified as ‘tolerant’. Any species in which incidence increased disproportionately with decreasing landscape-level tree cover (i.e. any one of the other six models was selected with a negative coefficient) was also identified as ‘tolerant’. Any species in which incidence decreased disproportionately with decreasing landscape tree cover (i.e. any one of the other six models was selected with a positive coefficient) was identified as a ‘decliner’.

Results

Of the 58 species, the null model fitted best for 21 species, the linear model for six species, the logarithmic model for four species, the quadratic model for four species and the change point model for 23 species. For two species (Tree Martin *Hirundo nigricans* and Striated Pardalote *Pardalotus striatus*), the change point model was selected but with a negative coefficient indicating higher incidence in landscapes with lower tree cover, so these two species were considered ‘tolerant’.

Following consideration of abundance and evenness of distribution across the study landscapes (see main text) 10 study species were chosen: two ‘tolerant’ species and eight

'decliners'. The two tolerant species were the White-plumed Honeyeater (*Lichenostomus penicillatus*), for which the null model was selected, and the Striated Pardalote, best described by the change point model with a negative coefficient (Table S1). Of the eight 'decliners', the change point model was selected for six species—Fuscous Honeyeater (*L. fuscus*), Grey Shrike-thrush (*Colluricincla harmonica*), Spotted Pardalote (*Pardalotus punctatus*), Superb Fairy-wren (*Malurus cyaeneus*), Weebill (*Smicronis brevirostris*) and Yellow-tufted Honeyeater (*L. melanops*). The Eastern Yellow Robin (*Eopsaltria australis*) showed a linear relationship. The quadratic model provided the best fit for the Brown Treecreeper (*Climacteris picumnus*) with highest incidence recorded in mid-cover (~30%) landscapes (Table A1). The decline in incidence of the Brown Treecreeper in landscapes above 30% tree cover was probably due to absence of suitable habitat (particularly hollow-bearing trees).

Table A1: AICc values and change point threshold in tree cover for species incidence model fitting

Species	Model							
	Null	Linear	Log	Quadratic	Power	Broken stick	Change point	Change point threshold value (%)
Brown Treecreeper	10.5	12.2	8.1	4.9	9.3	5.4	7.9	NA
Eastern Yellow Robin	26.0	4.1	13.6	5.5	6.6	7.3	5.1	NA
Fuscous Honeyeater	25.5	7.2	11.9	7.4	9.0	9.4	6.4	17.0
Grey Shrike-thrush	24.8	25.3	17.4	17.9	15.7	14.9	12.9	5.2
Superb Fairy-wren	7.5	2.8	2.4	4.5	4.9	7.1	1.9	18.1
Spotted Pardalote	22.8	3.7	4.2	1.2	3.6	4.1	-2.0	11.7
Striated Pardalote	4.0	4.7	3.8	6.7	6.7	8.0	3.3	9.9
Weebill	13.2	5.8	3.0	7.0	5.9	7.8	2.7	8.4
White-plumed Honeyeater	5.9	8.4	8.0	7.5	9.9	7.0	6.1	NA
Yellow-tufted Honeyeater	27.5	8.1	22.6	11.0	11.1	10.6	-4.4	7.8

Appendix B. MOBILITY INFORMATION FROM HANZAB

All data from Higgins et al. 2001, and Higgins and Peter 2002

Species	HANZAB précis	Mobility description and interpretive comments	Mobility classification
Brown Treecreeper (BT)	Sedentary. Some local dispersal, usually to adjacent territories. From 1953–1984, 1482 birds banded: seven recoveries away from original site of capture, all <10 km	Sedentary, sex-biased dispersal: males rarely disperse more than a few territories from natal site. Sedentary behaviour is corroborated by combination of high recovery rate, and no recoveries at >8 km. Additional radio-tracking and recapture data (V. Doerr unpublished) corroborate this view.	Sedentary
Eastern Yellow Robin (EYR)	Mainly sedentary or resident—some seasonal movements, particularly from higher altitude to plains in south-eastern Australia in winter	Mainly sedentary: inconclusive data. We believe EYR resident and sedentary within the study area. However, evidence of seasonal movements (often involving move to lower altitudes), and apparent influx of birds to some sites in the study area during winter. These may obscure underlying genetic structure of any resident population units, or, if some of these birds settle and interbreed, that may result in little or no IBD at the study-wide scale	Sedentary /inconclusive
Fuscous Honeyeater (FH)	Resident/partly resident, local abundance varies with influx when nectar plentiful, movements in and out of areas sometimes noted. Perhaps partially nomadic	Mobile, irregular seasonal movements with circumstantial evidence of large-scale movements (100s of km) in response to nectar resources. Only very small numbers present in some months during the field component of this project (unpublished data)	Mobile
Grey Shrike-thrush (GST)	Sedentary/resident with some local post-breeding dispersal. Described as nomadic or increasing in abundance in winter in some areas. Altitudinal movements from Alps in winter	Inconclusive, mostly sedentary; however, GST is a strong flyer, and combination of seasonal movements with post-breeding dispersal over unknown distances may weaken any isolation-by-distance	Moderate /Inconclusive

Species	HANZAB précis	Mobility description and interpretive comments	Mobility classification
Superb Fairy-wren (SFW)	Sedentary. dispersal of young, and, rarely, of female breeders short distances		Sedentary
Spotted Pardalote (SPP)	Apparently resident or sedentary in most of range though some regular possibly migratory movement is in south-eastern Australia. Variously considered mainly sedentary, resident or partly migratory. Movement inland or north from higher elevations in south-east of range in winter	Inconclusive, recorded as resident in habitat similar to the study area (Chiltern, to the east of our study, and also at Creswick, well to the west).	Moderate /Inconclusive
Striated Pardalote (STP)	Resident, migratory or dispersive, *P .s. ornatus* and *P. s. substriatus* in temperate areas resident dispersive or migratory, some inland northward movement in winter in south of range	.	Mobile
Weebill (WB)	Considered resident throughout range, some local movement, no regular seasonal movements		Moderate /Inconclusive
White-plumed Honeyeater (WPH)	Resident or sedentary, juveniles sometimes disperse widely from natal area, some (mainly local) movements to water in dry periods. No large-scale seasonal movements	Moderately mobile, probably less so than FH	Mobile

Species	HANZAB précis	Mobility description and interpretive comments	Mobility classification
Yellow-tufted Honeyeater (YTH)	Mainly resident or sedentary, with local movements, possibly larger scale movements (possibly in response to drought). *L.c. meltoni* most mobile, post-breeding dispersal in autumn or winter	Inconclusive, possibly moderately mobile. *L.c. meltoni*. The subspecies resident in the study area is anecdotally identified as most mobile subspecies	Moderate /Inconclusive

Appendix C. MEAN CORRELATION BETWEEN, AND CREDIBLE INTERVALS FOR ISOLATION MODELS

Isolation-by-resistance\ Circuitscape *vs*. least-cost distance						
						Isolation- by resistance
Correlation of uniform/IBD models						
UNIFORM		0.97 (0.902, 0.993)	0.903 (0.868, 0.937)		0.998 (0.997, 0.999)	
GEOG			0.809 (0.653, 0.927)			
logGEOG					0.807 (0.638, 0.926)	
Generic tree cover models						
TREE_25_10	0.477 (0.088, 0.791)	0.474 (0.095, 0.784)	0.425 (0.051, 0.734)		0.927 (0.889, 0.958)	0.571
TREE_25_100	0.327 (0.012, 0.697)	0.331 (0.012, 0.702)	0.294 (0.006, 0.632)		0.881 (0.822, 0.929)	0.419
TREE_25_2	0.818 (0.595, 0.937)	0.801 (0.586, 0.926)	0.737 (0.487, 0.891)		0.989 (0.982, 0.994)	0.862
TREE_25_5	0.577 (0.188, 0.837)	0.57 (0.193, 0.833)	0.515 (0.135, 0.785)		0.949 (0.922, 0.971)	0.666
Sedentary decliners						
BTC_EO_100	0.991 (0.976, 0.997)	0.966 (0.908, 0.992)	0.905 (0.845, 0.958)		0.999 (0.998, 0.999)	0.964
BTC_EO_5000	0.636 (0.229, 0.926)	0.638 (0.25, 0.92)	0.575 (0.157, 0.844)		0.918 (0.876, 0.955)	0.734
BTC_HAB_10	0.827 (0.577, 0.959)	0.831 (0.608, 0.957)	0.751 (0.491, 0.907)		0.921 (0.875, 0.96)	0.825
BTC_HAB_2	0.961 (0.902, 0.991)	0.943 (0.871, 0.984)	0.874 (0.784, 0.945)		0.994 (0.99, 0.997)	0.944
EYR_EO_100	0.979 (0.945, 0.994)	0.955 (0.892, 0.987)	0.893 (0.823, 0.952)		0.998 (0.997, 0.999)	0.956
EYR_EO_5000	0.236 (0, 0.788)	0.241 (0, 0.815)	0.214 (0.001, 0.704)		0.817 (0.724, 0.889)	0.442
EYR_HAB_10	0.469 (0.078, 0.787)	0.461 (0.077, 0.783)	0.416 (0.05, 0.729)		0.908 (0.857, 0.948)	0.541
EYR_HAB_2	0.816 (0.61, 0.939)	0.796 (0.58, 0.925)	0.735 (0.51, 0.889)		0.985 (0.977, 0.992)	0.850
SFW_EO_100	0.987 (0.966, 0.996)	0.962 (0.904, 0.99)	0.901 (0.837, 0.955)		0.998 (0.998, 0.999)	0.961
SFW_EO_5000	0.254 (0, 0.889)	0.258 (0, 0.909)	0.232 (0, 0.826)		0.845 (0.779, 0.9)	0.120
SFW_HAB_10	0.587 (0.214, 0.841)	0.591 (0.221, 0.845)	0.539 (0.142, 0.791)		0.905 (0.853, 0.947)	0.652
SFW_HAB_2	0.891 (0.746, 0.963)	0.877 (0.724, 0.961)	0.814 (0.649, 0.919)		0.99 (0.984, 0.995)	0.896
Intermediate/equivocal decliner						
GST_EO_100	0.991 (0.976, 0.998)	0.966 (0.908, 0.992)	0.905 (0.845, 0.958)		0.999 (0.998, 0.999)	0.964
GST_EO_5000	0.624 (0.204, 0.923)	0.627 (0.227, 0.919)	0.565 (0.135, 0.842)		0.913 (0.868, 0.952)	0.736
GST_HAB_10	0.596 (0.198, 0.86)	0.597 (0.205, 0.869)	0.545 (0.155, 0.808)		0.895 (0.838, 0.941)	0.681
GST_HAB_2	0.891 (0.722, 0.969)	0.874 (0.694, 0.961)	0.814 (0.633, 0.919)		0.989 (0.982, 0.994)	0.905
SPP_HAB_10	0.516 (0.112, 0.842)	0.519 (0.123, 0.853)	0.468 (0.078, 0.765)		0.906 (0.85, 0.947)	0.611
SPP_HAB_2	0.861 (0.688, 0.965)	0.844 (0.672, 0.959)	0.783 (0.58, 0.907)		0.986 (0.978, 0.992)	0.884
WB_EO_100	0.989 (0.973, 0.997)	0.905 (0.846, 0.958)	0.964 (0.893, 0.99)		0.999 (0.998, 0.999)	0.963
WB_EO_5000	0.595 (0.163, 0.927)	0.598 (0.166, 0.927)	0.542 (0.1, 0.857)		0.903 (0.855, 0.946)	0.727
WB_HAB_10	0.599 (0.195, 0.899)	0.606 (0.193, 0.913)	0.544 (0.145, 0.837)		0.892 (0.832, 0.94)	0.715
WB_HAB_2	0.899 (0.729, 0.979)	0.886 (0.714, 0.966)	0.816 (0.645, 0.923)		0.99 (0.984, 0.995)	0.917
Mobile decliners						
FH_EO_100	1 (1, 1)	0.974 (0.913, 0.996)	0.915 (0.865, 0.963)		0.998 (0.997, 0.999)	0.969
FH_EO_5000	0.688 (0.304, 0.935)	0.685 (0.322, 0.926)	0.62 (0.234, 0.855)		0.944 (0.914, 0.97)	0.762
FH_HAB_10	0.652 (0.281, 0.932)	0.651 (0.28, 0.929)	0.583 (0.2, 0.857)		0.907 (0.855, 0.951)	0.681
FH_HAB_2	0.918 (0.798, 0.983)	0.899 (0.77, 0.974)	0.826 (0.674, 0.922)		0.986 (0.978, 0.992)	0.908
YTH_EO_100	1 (1, 1)	0.974 (0.913, 0.996)	0.915 (0.865, 0.963)		0.998 (0.997, 0.999)	0.969
YTH_EO_5000	0.641 (0.24, 0.937)	0.641 (0.237, 0.936)	0.581 (0.165, 0.861)		0.924 (0.883, 0.958)	0.750
YTH_HAB_10	0.631 (0.231, 0.948)	0.63 (0.233, 0.941)	0.567 (0.145, 0.878)		0.904 (0.849, 0.948)	0.696
YTH_HAB_2	0.914 (0.786, 0.985)	0.895 (0.764, 0.977)	0.826 (0.661, 0.925)		0.989 (0.983, 0.994)	0.913
Mobile tolerant						
WPH_EO_100	1 (1, 1)	0.974 (0.912, 0.996)	0.915 (0.865, 0.963)		0.998 (0.997, 0.999)	0.969
WPH_EO_5000	0.784 (0.504, 0.957)	0.772 (0.492, 0.952)	0.709 (0.413, 0.891)		0.974 (0.96, 0.985)	0.818
WPH_HAB_10	0.795 (0.551, 0.936)	0.801 (0.567, 0.944)	0.732 (0.47, 0.888)		0.944 (0.912, 0.973)	0.828
WPH_HAB_2	0.957 (0.894, 0.988)	0.942 (0.867, 0.984)	0.876 (0.79, 0.951)		0.996 (0.993, 0.998)	0.947
Mean	0.75	0.736	0.680		0.949	0.782

Lower and Upper 95% credible intervals are given in brackets after mean Pearson R^2

Appendix D. Summary of Causal Modelling framework results for LCP&LCP_NULL and LCP&logGEOG with linearised F_{ST} and with individual genetic distances

Species abbreviations: BT, Brown Treecreeper; EYR, Eastern Yellow Robin; SFW, Superb Fairy-wren; YTH,Yellow-tufted Honeyeater.

Where a single best isolation-by-distance (IBD) or isolation-by-resistance (IBR) model was selected, it is listed. Where a causal modelling resulted in an indeterminate result, both IBD and the best IBR models are listed. Mantel and partial Mantel correlation (*r*) and *P* values are for the tests of IBR models with highest correlation (Mantel *r*) on marginal tests. Significant results are in bold

Table D1: Results for LCP & logGEOG for F_{ST}

				Marginal Mantel tests				Partial Mantel tests			
				IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
Species	Area	Inference	Best model(s) chosen	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
BT	Study	IBR	HAB_1_10	**0.274**	<0.001	**0.280**	<0.001	**0.080**	0.029	0.055	0.066
BT	East	-	-	0.122	0.110	0.135	0.147				
BT	West	IBD	IBD	**0.143**	0.009	0.106	0.100	−0.099	0.823	0.138	0.073
EYR	Study	-	-	0.230	0.088	0.273	0.056				
EYR	East	-	-	0.270	0.349	0.385	0.347				
SFW	Study	IBD/R	IBD/HAB_1_10	**0.323**	<0.001	**0.338**	<0.001	0.119	0.138	0.058	0.324
SFW	East	IBR	EO_5000	0.380	0.069	**0.503**	0.044	0.363	0.157	0.071	0.388
SFW	West	IBR	TH_10	**0.309**	0.010	**0.452**	0.002	**0.580**	0.008	−0.496	0.966
YTH	Study	-	-	−0.050	0.759	0.001	0.494				
YTH	East	-	-	−0.397	0.930	0.036	0.316				
YTH	West	-	-	−0.034	0.719	0.116	0.136				

Table D2: Results for individual genotypic distance (GD) with LCP &LCP.NULL

					Marginal Mantel tests				Partial Mantel tests			
					IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
Species	Sex	Area	Inference	Best model(s) chosen	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
BT	F	Study	IBR	TREE_1_100	**0.136**	<0.001	**0.151**	<0.001	**0.075**	0.007	−0.034	0.867
	M	Study	IBD/R	IBD/HAB_1_10	**0.131**	<0.001	**0.130**	<0.001	0.008	0.350	0.017	0.212
	ALL	Study	IBR	EO_5000	**0.128**	<0.001	**0.132**	<0.001	**0.030**	0.049	0.001	0.485
	F	East	-	-	0.036	0.253	0.029	0.293				
	M	East	IBD/R	IBD/HAB_1_10	**0.146**	<0.001	**0.151**	<0.001	0.037	0.227	−0.001	0.522
	ALL	East	IBD/R	IBD/EO_100	**0.085**	0.001	**0.084**	0.002	−0.026	0.760	0.029	0.213
	F	West	IBR	EO_5000	0.028	0.154	**0.087**	<0.001	**0.105**	0.006	−0.066	0.934
	M	West	IBD	IBD	**0.117**	<0.001	**0.114**	<0.001	−0.044	0.971	**0.051**	0.016
	ALL	West	IBD/R	IBD/EO_100	**0.073**	<0.001	**0.073**	<0.001	0	0.505	0.005	0.377
EYR	F	Study	-	-	0.022	0.270	0.038	0.128				
	M	Study	IBR	TREE_1_100	0.048	0.067	**0.065**	0.020				
	ALL	Study	IBD/R	IBD/TREE_1_100	**0.036**	0.042	**0.052**	0.005	0.059	0.076	−0.047	0.855
	F	East	-	-	−0.002	0.501	0.031	0.396				
	M	East	-	-	−0.082	0.791	-0.054	0.649				
	ALL	East	-	-	−0.051	0.756	-0.016	0.565				
	F	West	-	-	0.040	0.297	0.027	0.350				
	M	West	-	-	0.033	0.323	0.027	0.358				
	ALL	West	-	-	0.047	0.164	0.041	0.187				

					Marginal Mantel tests				Partial Mantel tests			
					IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
Species	Sex	Area	Inference	Best model(s) chosen	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
SFW	F	Study	IBD/R	IBD/EO_5000	**0.075**	0.018	**0.090**	<0.001	0.051	0.154	−0.009	0.569
	M	Study	IBR	HAB_1_10	**0.165**	<0.001	**0.193**	<0.001	**0.117**	0.003	−0.061	0.904
	ALL	Study	IBR	HAB_1_10	**0.132**	<0.001	**0.154**	<0.001	**0.096**	0.001	−0.052	0.934
	F	East	IBD/R	IBD/HAB_1_2	**0.066**	0.043	**0.067**	0.032	0.014	0.394	−0.005	0.541
	M	East	IBD/R	IBD/TREE_1_10	**0.146**	0.001	**0.176**	<0.001	0.105	0.053	−0.035	0.711
	ALL	East	IBD/R	IBD/TREE_1_10	**0.108**	<0.001	**0.120**	<0.001	0.052	0.101	−0.001	0.510
	F	West	IBD/R	IBD/EO_100	**0.197**	0.001	**0.194**	0.001	-0.048	0.752	0.059	0.193
	M	West	IBD/R	IBD/HAB_1_10	**0.222**	<0.001	**0.232**	<0.001	0.070	0.151	0.000	0.497
	ALL	West	IBD/R	IBD/EO_100	**0.210**	<0.001	**0.209**	<0.001	-0.024	0.765	0.035	0.151
YTH	F	Study	-	-	0.010	0.394	0.014	0.336				
	M	Study	-	-	0.016	0.292	0.018	0.257				
	ALL	Study	-	-	0.011	0.298	0.016	0.240				
	F	East	-	-	−0.015	0.627	−0.017	0.610				
	M	East	-	-	0.070	0.122	0.106	0.090				
	ALL	East	-	-	0.012	0.361	0.042	0.247				
	F	West	IBR	TREE_1_100	**0.036**	0.022	**0.078**	0.007	**0.079**	0.026	−0.039	0.885
	M	West	IBR	TREE_1_100	0.013	0.072	**0.043**	0.015				
	ALL	West	IBR	TREE_1_100	**0.019**	0.009	**0.054**	0.001	**0.064**	0.004	−0.040	0.984

Table D3: Results for LCP & LCP.NULL for F_{ST}

				Marginal Mantel tests				Partial Mantel tests			
				IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
Species	Area	Inference	Best model(s) chosen	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
BT	Study	IBD_R	IBD/HAB_1_10	**0.264**	<0.001	**0.280**	<0.001	0.104	0.057	−0.042	0.719
BT	East	-	-	0.136	0.140	0.135	0.140				
BT	West	-	-	0.114	0.082	0.106	0.100				
EYR	Study	-	-	0.175	0.131	0.273	0.057				
EYR	East	-	-	0.309	0.328	0.385	0.349				
SFW	Study	IBD_R	IBD/HAB_1_10	**0.277**	0.004	**0.338**	<0.001	0.270	0.054	−0.183	0.827
SFW	East	IBR	EO_5000	0.320	0.142	**0.503**	0.047				
SFW	West	IBR	HAB_1_10	**0.322**	0.018	**0.452**	0.001	**0.699**	0.007	−0.652	0.984
YTH	Study	-	-	0.000	0.491	0.001	0.480				
YTH	East	-	-	−0.404	0.957	0.036	0.327				
YTH	West	-	-	0.051	0.217	0.116	0.136				

Table D4: Results for individual genotypic distance (GD) with LCP &logGEOG

					Marginal Mantel tests				Partial Mantel tests			
					IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
Species	Sex	Area	Inference	Best model(s) chosen	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
BT	F	Study	IBR	TREE_1_100	**0.127**	<0.001	**0.151**	<0.001	**0.083**	<0.001	0.006	0.344
	M	Study	IBD	IBD	**0.161**	<0.001	**0.130**	<0.001	−0.014	0.846	**0.097**	<0.001
	ALL	Study	IBD	IBD	**0.139**	<0.001	**0.132**	<0.001	**0.028**	0.016	**0.054**	<0.001
	F	East	-	-	0.034	0.204	0.029	0.299				
	M	East	IBD	IBD	**0.222**	<0.001	**0.151**	<0.001	−0.082	0.984	**0.184**	<0.001
	ALL	East	IBD	IBD	**0.130**	<0.001	**0.084**	0.001	−0.061	0.991	**0.117**	<0.001
	F	West	IBR	EO_5000	**0.054**	0.002	**0.087**	<0.001	**0.074**	0.032	−0.029	0.783
	M	West	IBD	IBD	**0.131**	<0.001	**0.114**	<0.001	−0.012	0.666	**0.066**	0.001
	ALL	West	IBD	IBD	**0.092**	<0.001	**0.073**	<0.001	−0.026	0.893	**0.063**	<0.001
EYR	F	Study	-	-	0.031	0.218	0.038	0.122				
	M	Study	IBD/R	IBD/TREE_1_100	**0.057**	0.047	**0.065**	0.017	0.032	0.209	0.006	0.438
	ALL	Study	IBD/R	IBD/TREE_1_100	**0.049**	0.018	**0.052**	0.004	0.019	0.235	0.012	0.342
	F	East	-	-	0.034	0.390	0.031	0.407				
	M	East	-	-	−0.029	0.622	−0.054	0.659				
	ALL	East	-	-	0.001	0.494	−0.016	0.555				
	F	West	-	-	0.033	0.311	0.027	0.350				
	M	West	-	-	0.099	0.068	0.027	0.360				
	ALL	West	IBD	IBD	**0.081**	0.015	0.041	0.195	−0.072	0.892		

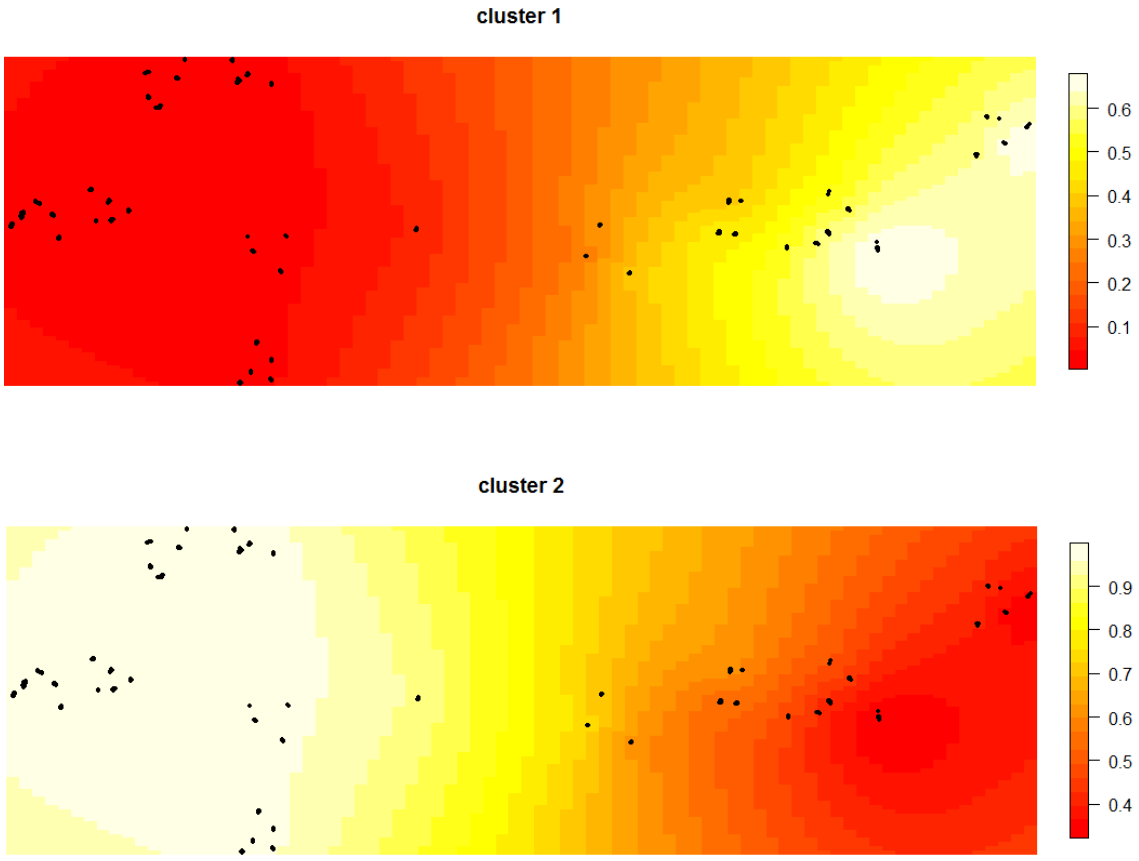
					Marginal Mantel tests				Partial Mantel tests			
					IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
Species	Sex	Area	Inference	Best model(s) chosen	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
SFW	F	Study	IBD	IBD	**0.111**	<0.001	**0.090**	<0.001	0.007	0.408	**0.065**	0.026
	M	Study	IBD	IBD	**0.206**	<0.001	**0.193**	<0.001	**0.047**	0.023	**0.087**	<0.001
	ALL	Study	IBD	IBD	**0.164**	<0.001	**0.154**	<0.001	**0.039**	0.009	**0.068**	<0.001
	F	East	IBD/R	IBD TH_2	**0.091**	0.001	**0.067**	0.037	−0.023	0.650	0.066	0.102
	M	East	IBR	TREE_1_10	**0.107**	<0.001	**0.176**	<0.001	**0.152**	0.015	−0.057	0.831
	ALL	East	IBD/R	IBD/TREE_1_10	**0.101**	<0.001	**0.120**	<0.001	0.065	0.078	0.009	0.401
	F	West	IBD/R	IBD/EO_100	**0.217**	0.001	**0.194**	0.002	−0.020	0.616	0.101	0.057
	M	West	IBD	IBD	**0.295**	<0.001	**0.232**	<0.001	−0.088	0.905	**0.205**	<0.001
	ALL	West	IBD	IBD	**0.256**	<0.001	**0.209**	<0.001	−0.069	0.981	**0.166**	<0.001
YTH	F	Study	-	-	0.012	0.315	0.014	0.336				
	M	Study	-	-	0.015	0.190	0.018	0.259				
	ALL	Study	-	-	0.009	0.270	0.016	0.234				
	F	East	-	-	0.069	0.056	−0.017	0.614				
	M	East	-	-	0.062	0.068	0.106	0.094				
	ALL	East	IBD	IBD	**0.037**	0.046	0.042	0.255				
	F	West	IBR	TREE_1_100	0.021	0.120	**0.078**	0.007				
	M	West	IBR	TREE_1_100	**0.013**	0.039	**0.043**	0.014	**0.049**	0.049	−0.027	0.876
	ALL	West	IBR	TREE_1_100	0.009	0.081	**0.054**	<0.001				

Appendix E. TESS ANALYSIS FOR BROWN TREECREEPER AND SUPERB FAIRY-WREN

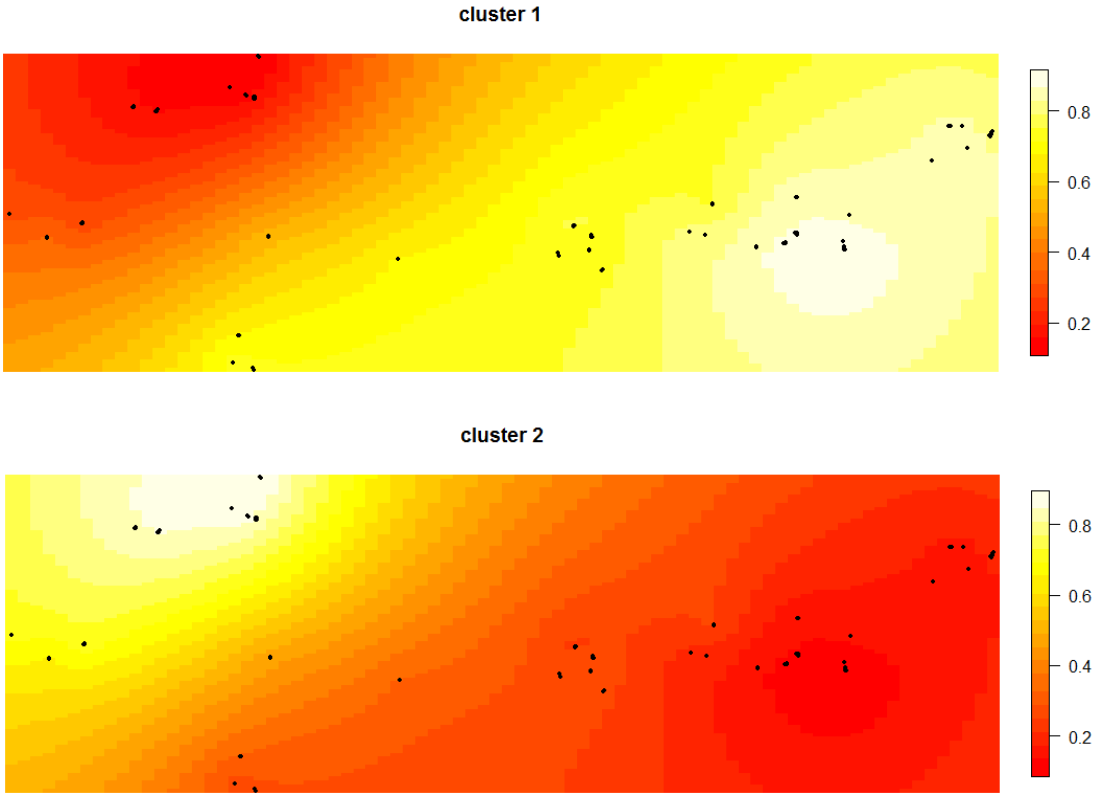
We used Bayesian spatial algorithm implemented in TESS 2.3.1 (Chen et al. 2007) to assess the presence of study-wide population subdivision within cooperative breeders and the least mobile species in our dataset, Brown Treecreeper and Superb Fairy-wren. TESS was run using genotypic data (12 loci for Brown Treecreeper and 11 for Superb Fairy-wren) assuming two genetic clusters ($K = 2$) using the CAR admixture model with spatial interaction parameter $P = 0.6$. A total of 100 replicates of 3×10^4 burn-in sweeps followed by 10^6 sweeps were run for each species, then 10 replicates with lowest DIC were averaged using the Greedy algorithm option with 1000 random input orders in CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and interpolated and plotted using R script provided in the TESS manual. Finer genetic structure ($K > 2$) for Superb Fairy-wren is explored in Harrisson et al. (2013), and for Brown Treecreeper will be explored elsewhere (Pavlova et al. unpublished data).

Both Brown Treecreeper (Fig. S3A) and Superb Fairy-wren (Fig. S3B) showed the presence of the overall east–west structure across the study area with probabilities of Cluster 1 in the east and Cluster 2 in the west in both species, although the geographic details of the population subdivision differed between species.

Supplementary Figure S3A: Spatial interpolation of admixture proportions for two genetic clusters (K = 2) detected by TESS from genotypes of Brown Treecreeper across the Box–Ironbark region of north-central Victoria. Black dots indicate sampled individuals clustered into sites (distributed on the plots roughly according to their latitudinal/longitudinal positions); bars show genetic cluster probabilities



Supplementary Figure S3B: Spatial interpolation of admixture proportions for two genetic clusters (K = 2) detected by TESS from genotypes of Superb Fairy-wren across the Box–Ironbark region of north-central Victoria. Black dots indicate sampled individuals clustered into sites (distributed on the plots roughly according to their latitudinal/longitudinal positions); bars show genetic cluster probabilities



Appendix F. FRAGSTATS CLASS AGGREGATION STATISTICS FOR TREE COVER IN EAST AND WEST

Indices of tree cover aggregation calculated from 25-m pixel tree cover raster for the east and west zone in FRAGSTATS ver. 4 (McGarigal et al. 2012) indicating whether the indices support that the east zone is more aggregated than the west

FRAGSTATS Metric	Zone		Support for east being more aggregated; west more fragmented and dispersed
	East	West	
Number of patches	4836	8299	Yes
Patch density	3.94	4.11	Yes
Landscape shape index	35.88	65.89	Yes
CLUMPY	0.935	0.905	Yes
PLADJ	95.74	93.18	Yes (marginal)
COHESION	99.41	99.51	NIL
DIVISION	0.932	0.987	Yes
MESH	8385	2673	Yes
SPLIT	14.63	75.47	Yes
Aggregation index	95.85	93.27	Yes (marginal)
Normalised landscape shape index)	0.0415	0.0673	Yes

Appendix G. BUILDING CIRCUITSCAPE ISOLATION-BY-RESISTANCE AND ISOLATION-BY-DISTANCE MODELS

Values used for building resistance surfaces for each landscape model are given in Table C1. A null model of isolation-by-distance (IBD) was built using a surface with uniform resistance. Resistance surfaces for isolation-by-resistance (IBR) models comprised three groups: (i) a set of three general models in which resistance of tree cover to dispersal was set to 1 and resistance of all other land cover classes to 2, 10 or 100 (models TREE_1_2, TREE_1_10, and TREE_1_100, respectively), (ii) two species-specific models per species based on expert opinion of resistances for six land cover classes (native tree cover, horticulture/pine, unimproved pasture with scattered trees, crop/improved pasture with scattered trees, cleared land without scattered trees, urban) to a dispersal event of 100 m (EO_100) or 5 km (EO_5000) during the lifetime of an individual bird (EO_100 models for the three honeyeaters were indistinguishable from IBD and are not tested here; EO models for the two pardalotes were not built), and (iii) two models based on a binary species-specific distribution model of habitat *vs*. non-habitat in which the resistance of habitat was set to 1 and resistance of non-habitat to 2 or 10 (HAB_1_2 and HAB_1_10, respectively). Correlations between the matrices, and the expected order of strength of correlation between the landscape resistance matrices and pairwise genetic distance for each species across the study area are tabulated in Amos et al. (2012).

Table G1: Values used for building resistance surfaces for each landscape model (modified from Amos et al. 2012)

Model groups	Resistance surface/ model code	Native tree cover	Horticulture/ pine	Unimproved pasture with scattered trees	Crop/improved pasture with scattered trees	Cleared land no scattered trees	Urban	All land cover	Trees	Probable habitat	All other cells
IBD	UNIFORM							1			
Tree cover	TREE_1_2								1		2
	TREE_1_5								1		5
	TREE_1_10								1		10
	TREE_1_100								1		100

Model groups	Resistance surface/ model code	Native tree cover	Horticulture/ pine	Unimproved pasture with scattered trees	Crop/improved pasture with scattered trees	Cleared land no scattered trees	Urban	All land cover	Trees	Probable habitat	All other cells
Habitat suitability[1]	HAB_1_2									1	2
	HAB_1_10									1	10
Expert opinion[2]	BT_EO_100	1	2000	1.2	1.2	2000	2000				
	BT_EO_5000	3.07	8000	4000	6000	8000	8000				
	EYR_EO_100	1	1.3	1.3	1.3	2000	2000				
	EYR_EO_5000	2000	6010	6010	8000	10000	10000				
	FH_EO_5000	2.17	2010	2010	2010	4010	4010				
	GST_EO_100	1	1.3	1.13	1.3	2000	1.8				
	GST_EO_5000	2.9	2000	7.17	2010	6010	6010				
	SFW_EO_100	1	1.02	2000	2000	2000	1.8				
	SFW_EO_5000	2000	6000	10,000	10,000	10,000	10,000				
	WB_EO_100	1	1.8	1.8	1.8	2000	1.3				
	WB_EO_5000	11.6	6010	4000	4000	8000	8000				
	WPH_EO_5000	2.62	10.1	5.6	6.32	2010	7.45				
	YTH_EO_5000	2.17	2010	2010	2010	6010	6010				

Appendix H. PARENTAGE ANALYSIS FOR BROWN TREECREEPER

Including offspring of sampled parents in analyses assuming a random sample of unrelated individuals can bias results and lead to incorrect inferences. We performed parentage assignment analysis using CERVUS 3.0.3 (Kalinowski et al. 2007) on 621 individuals that were genotyped for at least 11 of 12 available loci, to identify and remove from the analyses all but one member of all parent–offspring pairs. Analysis was performed on the scale of the whole study area. Candidate mothers included 202 adult females and five females of unknown age; candidate fathers, 267 adult and three unknown age males; and all individuals were included as candidate offspring. The confidence of the assignment was assessed by simulating genotypes of 5000 parents (mothers or fathers) and 100,000 offspring, assuming 0.1 is the proportion of parents sampled; 0.998, the proportion of typed loci; and 0.01, the proportion of mistyped loci. With these settings, CERVUS detected 15 mother–offspring and nine father–offspring pairs with 80% confidence (Supplementary Table S1). The 24 individuals identified as offspring (column 1 in Supplementary Table S1) were removed from analyses.

Appendix H Table 1. Maternity and paternity assignments from CERVUS. LOD score, the natural log of the overall likelihood ratio; Delta, the difference in LOD scores between the most likely candidate parent and the second most likely candidate parent pair confidence; *, 95%; +, 80%.

Offspring					Assigned mother (F) or father (M)					No. loci typed	No. pairs of loci compared	No. pairs of loci mismatching	Pair LOD score	Pair Delta	Pair confidence
LabID	Site	NetID	Age	Sex	LabID	Site	NetID	Age	Sex						
BT036	Ha2	N108	A	M	BT139	Ha2	N205	A	F	12	12	0	8.33E+00	8.33E+00	+
BT093	Mu1	N103	J	F	BT095	Mu1	N104	A	F	12	12	0	8.15E+00	7.05E+00	+
BT126	Cr1	N202	A	M	BT121	Cr1	N203	A	F	12	12	0	1.16E+01	1.09E+01	*
BT179	Mu1	N214	A	M	BT098	Mu1	N106	A	F	12	12	0	1.48E+01	1.29E+01	*
BT199	We2	N211	A	M	BT112	We2	N110	A	F	12	12	0	9.91E+00	7.45E+00	+
BT215	Ax4	N104	I	F	BT213	Ax4	N106	A	F	12	12	0	9.83E+00	9.39E+00	*
BT225	Cr3	N117	J	M	BT304	Cr3	N218	A	F	12	12	0	9.23E+00	8.50E+00	+
BT236	Ha4	N106	A	F	BT237	Ha4	N105	A	F	12	12	0	1.05E+01	7.38E+00	+
BT280	St3	N106	I	M	BT470	St3	N205	A	F	12	12	0	1.19E+01	8.18E+00	+
BT294	St4	N113	I	F	BT295	St4	N113	A	F	12	12	0	9.09E+00	7.29E+00	+

Offspring					Assigned mother (F) or father (M)					No. loci typed	No. pairs of loci compared	No. pairs of loci mismatching	Pair LOD score	Pair Delta	Pair confidence
LabID	Site	NetID	Age	Sex	LabID	Site	NetID	Age	Sex						
BT538	We6	N203	A	M	BT357	We6	N116	A	F	12	12	0	8.17E+00	8.03E+00	+
BT539	We6	N203	J	M	BT357	We6	N116	A	F	12	12	0	1.17E+01	9.18E+00	*
BT602	St5	N207	I	M	BT605	St5	N207	A	F	12	12	1	8.28E+00	8.28E+00	+
BT617	Gl4	N208	I	M	BT632	Gl4	N212	A	F	12	12	0	1.12E+01	1.12E+01	*
BT621	Gl4	N213	I	F	BT632	Gl4	N212	A	F	12	12	0	7.97E+00	7.97E+00	+
BT037	Ha2	N108	A	M	BT036	Ha2	N108	A	M	12	12	0	9.76E+00	8.30E+00	+
BT048	Tu1	N112	J	F	BT049	Tu1	N118	A	M	12	12	0	9.06E+00	7.38E+00	+
BT121	Cr1	N203	A	F	BT126	Cr1	N202	A	M	12	12	0	1.16E+01	9.31E+00	*
BT149	Du1	N206	A	F	BT150	Du1	N206	A	M	12	12	0	7.57E+00	7.08E+00	+
BT333	Ha6	N102	I	F	BT336	Ha6	N106	A	M	12	12	1	8.83E+00	8.71E+00	+
BT591	Re4	N213	A	M	BT592	Re4	N213	A	M	12	12	0	9.19E+00	7.76E+00	+
BT594	Re4	N213	I	M	BT592	Re4	N213	A	M	12	12	0	8.78E+00	7.98E+00	+

Offspring					Assigned mother (F) or father (M)					No. loci typed	No. pairs of loci compared	No. pairs of loci mismatching	Pair LOD score	Pair Delta	Pair confidence
LabID	Site	NetID	Age	Sex	LabID	Site	NetID	Age	Sex						
BT617	Gl4	N208	I	M	BT633	Gl4	N213	A	M	12	12	0	1.10E+01	7.89E+00	+
BT629	Gl4	N208	A	F	BT359	Gl2	N104	A	M	12	12	0	8.50E+00	7.46E+00	+

Appendix I. NUMBER OF ADULTS WITH COMPLETE GENOTYPE FOR EACH SPECIES, ZONE, SITE AND SEX

		Brown Treecreeper			Eastern Yellow Robin			Fuscous Honeyeater			Grey Shrike-thrush			Superb Fairy-wren		
Zone	Sex	F	M	Total	F	M	Total	F	M	Total	F	M	Total	F	M	Total
East	Re1	4	6	10	7	6	13	1	7	8		2	2	3	2	5
	Re2	5	3	8	2	4	6	10	8	18	2	1	3			
	Re3	7	2	9	1	1	2	6	10	16	1	1	2	3	2	5
	Re4	6	11	17	1	6	7	14	18	32				3	2	5
	Re5	2	2	4		2	2	1		1				2	3	5
	Ru1															
	Ru2													1	3	4
	Ru3	1		1				6	11	17	2	1	3	1	2	3
	Ru4	1	6	7	1	1	2	3	4	7		1	1	3	5	8
	Ax1	5	2	7	1	2	3	4	7	11		2	2	1	1	2
	Ax3										1	2	3	3	4	7
	Ax4	1	1	2							1	1	2	10	9	19
	Ax5											1	1	1	2	3
	Ax6	1	1	2	1	1	2	4	13	17		2	2	3		3
	Ax7															
	Cr1	1	9	10	1	2	3	13	10	23	1	1	2	1	1	2
	Cr2	4	14	18				6	8	14						
	Cr3	4	6	10		1	1	16	13	29				1	1	2
	Cr4	2	3	5				2	1	3				5	4	9
	Cr5															
	Mu1	4	6	10	1	1	2							9	9	18
	Mu2	4	7	11	1	2	3	5	16	21	1		1		1	1
	Mu3	2	3	5	1		1					1	1	1		1
	Mu4	1	5	6		3	3				1		1	3	1	4
	Mu5	3	3	6	1	2	3							1	1	2
East total		**58**	**90**	**148**	**19**	**34**	**53**	**91**	**126**	**217**	**10**	**16**	**26**	**55**	**53**	**108**

		Brown Treecreeper			Eastern Yellow Robin			Fuscous Honeyeater			Grey Shrike-thrush			Superb Fairy-wren		
Zone	Sex	F	M	Total	F	M	Total	F	M	Total	F	M	Total	F	M	Total
West	Du1	1	4	5				16	19	35						
	Du2	3	4	7	1	1	2	11	14	25						
	Du3		1	1												
	Du4		1	1							1	1	2	1	1	2
	Ha1	6	3	9	1	1	2	3	10	13	2		2			
	Ha2	5	4	9				8	13	21	3		3			
	Ha3								2	2						
	Ha4	8	7	15	2	2	4				2	2	4	7	3	10
	Ha5	2	3	5				3	6	9	1		1	3	3	6
	Ha6	5	10	15	1		1	1	3	4		1	1	1	3	4
	St1	9	12	21				1	1	2						
	St2	3	6	9	4	2	6	2	10	12				3	2	5
	St3	6	10	16	1	1	2									
	St4	5	5	10				4	3	7		1	1			
	St5	16	11	27		2	2		1	1					1	1
	St7															
	Tu1	3	4	7												
	Tu2	6	11	17				1	1	2						
	Tu3	5	6	11							1		1	5	6	11
	Tu4	6	5	11	2	3	5									
	Tu5	3	4	7		1	1	2	3	5						
	Gl1	4	8	12		1	1	5	2	7		3	3			
	Gl2	3	8	11	1	1	2					1	1			
	Gl3	2	2	4	1	1	2	1		1	1	3	4	2	5	7
	Gl4	13	12	25	2	4	6					1	1			
	Gl5													2	6	8
	Gl6														7	7
	We1											1	1	1	3	4
	We2	9	10	19							1	2	3			
	We3	9	9	18	1	1	2	1	3	4						
	We4	5	7	12								1	1			
	We5	4	5	9	2	3	5	2	4	6		1	1			
	We6	2	6	8	1	2	3	1	5	6	1	1	2	1	1	2
West total		**143**	**178**	**321**	**20**	**26**	**46**	**62**	**100**	**162**	**13**	**19**	**32**	**26**	**41**	**67**
Sh	Sh1	2	3	5		3	3	16	26	42		1	1			
	Sh2															
	Sh3															
	Sh4														1	1
Overall totals		**203**	**271**	**474**	**39**	**63**	**102**	**169**	**252**	**421**	**23**	**36**	**59**	**81**	**95**	**176**

		Spotted Pardalote			Striated Pardalote			Weebill			White-plumed Honeyeater			Yellow-tufted Honeyeater		
Zone	Sex	F	M	Total	F	M	Total	F	M	Total	F	M	Total	F	M	Total
East	Re1					1	1									
	Re2								1	1	1		1	4	8	12
	Re3		1	1	1	3	4				3	6	9	2	3	5
	Re4				1		1							3	3	6
	Re5							2	2	4					1	1
	Ru1		2	2												
	Ru2	4	4	8				1	1	2						
	Ru3	1	6	7					2	2		2	2	1		1
	Ru4				2	3	5					1	1		1	1
	Ax1													3	1	4
	Ax3															
	Ax4	1	1	2	6	3	9					7	7			
	Ax5	7	3	10	2	3	5	1	3	4						
	Ax6				1	1	2		1	1						
	Ax7				2	3	5									
	Cr1				1		1	1	1	2		1	1	8	12	20
	Cr2		1	1	1	2	3							3	10	13
	Cr3	2	3	5	1	1	2	1	3	4	1	2	3			
	Cr4	1	3	4		2	2		1	1	3	7	10			
	Cr5							1		1						
	Mu1					1	1					13	13			
	Mu2				1		1				1		1	13	10	23
	Mu3	1	1	2		3	3	6	8	14	6	7	13			
	Mu4		1	1	1	2	3		1	1	1	6	7			
	Mu5	1		1				1	4	5	3	5	8			
East total		**18**	**26**	**44**	**20**	**28**	**48**	**14**	**28**	**42**	**19**	**57**	**76**	**37**	**49**	**86**

		Spotted Pardalote			Striated Pardalote			Weebill			White-plumed Honeyeater			Yellow-tufted Honeyeater		
Zone	Sex	F	M	Total	F	M	Total	F	M	Total	F	M	Total	F	M	Total
West	Du1				2	1	3							28	30	58
	Du2															
	Du3	1	1	2					2	2				3	7	10
	Du4	1		1					4	4				2	6	8
	Ha1										2	8	10	3	10	13
	Ha2				1	1	2				1		1	1	4	5
	Ha3															
	Ha4								1	1		1	1	14	25	39
	Ha5							2		2		3	3	3	3	6
	Ha6	1	1	2		1	1							9	14	23
	St1										2	13	15	6	20	26
	St2							2	1	3	2	3	5	5	5	10
	St3				2		2				3	5	8	6	15	21
	St4					1	1		1	1	3	8	11	17	17	34
	St5		1	1								1	1	5	18	23
	St7				7	9	16									
	Tu1										2	8	10			
	Tu2										3	8	11			
	Tu3										5	8	13			
	Tu4										1	11	12	2	3	5
	Tu5										3	11	14	2	2	4
	Gl1				1		1				2	6	8	7	18	25
	Gl2	1		1							4	8	12	5	9	14
	Gl3							4	3	7	1		1	4	11	15
	Gl4											2	2	4	15	19
	Gl5										1	3	4			
	Gl6										1		1			
	We1	1		1		1	1	1	2	3						
	We2										5	7	12	7	3	10
	We3										4	10	14			
	We4				1	1	2				3	8	11			
	We5							1	2	3	2	2	4		2	2
	We6											8	8	3	2	5
West total		**5**	**3**	**8**	**14**	**15**	**29**	**10**	**16**	**26**	**50**	**142**	**192**	**136**	**239**	**375**
Sh	Sh1				2	2	4	1	2	3	1	6	7	1	9	10
	Sh2		1	1		2	2	1	2	3						
	Sh3				4	6	10									
	Sh4															
Overall totals		**23**	**30**	**53**	**40**	**53**	**93**	**26**	**48**	**74**	**70**	**205**	**275**	**174**	**297**	**471**

Appendix J. MARGINAL MANTEL TESTS FOR F_{ST} AND INDIVIDUAL GENETIC DISTANCES FOR ALL MODELS

Table J1. Marginal Mantel test results for F_{ST} for all models. Tests were performed for species and area combinations where >5 sites each had five or more individual sampled. Significant tests are shown in bold

		Study		East		West	
Species	Model	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*
Brown Treecreeper	IBD	**0.269**	<0.001	0.124	0.124	**0.129**	0.024
	EO_100	**0.263**	<0.001	0.146	0.098	**0.119**	0.031
	EO_5000	**0.178**	0.022	0.221	0.109	0.019	0.399
	HAB_1_2	**0.260**	<0.001	0.175	0.089	0.123	0.076
	HAB_1_10	**0.233**	<0.001	0.201	0.109	0.079	0.239
	TREE_1_2	**0.204**	0.003	0.171	0.145	0.036	0.378
	TREE_1_10	0.110	0.127	0.155	0.227	−0.023	0.543
	TREE_1_100	0.062	0.280	0.104	0.314	−0.030	0.553
Eastern Yellow Robin	IBD	0.181	0.136	0.278	0.320		
	EO_100	**0.294**	0.048	0.280	0.330		
	EO_5000	**0.732**	0.028	0.374	0.347		
	HAB_1_2	**0.370**	0.029	0.288	0.333		
	HAB_1_10	**0.548**	0.023	0.332	0.374		
	TREE_1_2	**0.390**	0.023	0.297	0.334		
	TREE_1_10	**0.568**	0.022	0.340	0.348		
	TREE_1_100	**0.639**	0.022	0.379	0.351		
Fuscous Honeyeater	IBD	0.069	0.115	0.144	0.202	0.038	0.355
	EO_5000	0.155	0.073	0.100	0.303	0.148	0.178
	HAB_1_10	0.141	0.072	0.091	0.312	0.127	0.208
	TREE_1_2	0.157	0.056	0.128	0.235	0.156	0.175
	TREE_1_10	0.215	0.061	0.111	0.286	0.175	0.174
	TREE_1_100	0.230	0.058	0.093	0.340	0.179	0.174
Superb Fairy-wren	IBD	**0.275**	0.012	0.363	0.095	**0.318**	0.012
	EO_100	**0.318**	0.002	0.427	0.067	**0.372**	0.002
	EO_5000	**0.229**	0.001	**0.528**	0.029	0.129	0.364

		Study		East		West	
Species	Model	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*
	HAB_1_2	**0.420**	0.002	0.430	0.071	**0.481**	0.021
	HAB_1_10	**0.567**	0.001	**0.494**	0.049	**0.610**	0.034
	TREE_1_2	**0.446**	0.001	**0.613**	0.018	**0.532**	0.016
	TREE_1_10	**0.532**	0.002	**0.714**	0.006	0.536	0.093
	TREE_1_100	**0.542**	0.007	**0.739**	0.006	0.486	0.147
Striated Pardalote	IBD	0.305	0.095	**0.702**	0.032		
	TREE_1_2	0.312	0.124	**0.791**	0.049		
	TREE_1_10	0.263	0.180	**0.821**	0.048		
	TREE_1_100	0.215	0.236	0.832	0.050		
White-plumed Honeyeater	IBD	−0.016	0.532	0.291	0.069	0.212	0.053
	EO_5000	−0.156	0.933	0.202	0.154	−0.162	0.828
	HAB_1_10	−0.130	0.919	0.155	0.204	−0.133	0.794
	TREE_1_2	−0.089	0.791	0.097	0.303	0.009	0.488
	TREE_1_10	−0.172	0.908	−0.123	0.697	−0.145	0.761
	TREE_1_100	−0.217	0.939	−0.274	0.862	−0.203	0.846
Yellow-tufted Honeyeater	IBD	−0.022	0.597	−0.405	0.966	−0.012	0.561
	EO_5000	0.006	0.470	−0.175	0.728	0.085	0.152
	HAB_1_10	0.003	0.481	−0.294	0.877	0.056	0.261
	TREE_1_2	0.092	0.134	−0.374	0.944	**0.230**	0.018
	TREE_1_10	**0.185**	0.025	−0.263	0.864	**0.336**	0.007
	TREE_1_100	**0.206**	0.020	−0.018	0.418	**0.340**	0.009

Table J2: Marginal Mantel tests for individual genotypic distance for all models. Significant tests are shown in bold

Species		Study area						East						West					
	Sex	ALL		F		M		ALL		F		M		ALL		F		M	
	Model	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*
Brown Treecreeper	IBD	**0.142**	<0.001	**0.134**	<0.001	**0.162**	<0.001	**0.147**	<0.001	0.042	0.107	**0.246**	<0.001	**0.097**	<0.001	**0.062**	<0.001	**0.135**	<0.001
	EO_100	**0.143**	<0.001	**0.141**	<0.001	**0.157**	<0.001	**0.144**	<0.001	0.042	0.129	**0.242**	<0.001	**0.102**	<0.001	**0.073**	<0.001	**0.135**	<0.001
	EO_5000	**0.131**	<0.001	**0.179**	<0.001	**0.103**	<0.001	**0.092**	0.002	0.023	0.349	**0.155**	<0.001	**0.105**	0.001	**0.157**	0.001	**0.071**	0.046
	HAB_1_2	**0.143**	<0.001	**0.151**	<0.001	**0.149**	<0.001	**0.143**	<0.001	0.046	0.125	**0.236**	<0.001	**0.109**	<0.001	**0.090**	<0.001	**0.135**	<0.001
	HAB_1_10	**0.138**	<0.001	**0.169**	<0.001	**0.125**	<0.001	**0.126**	<0.001	0.038	0.239	**0.206**	<0.001	**0.115**	<0.001	**0.136**	<0.001	**0.108**	<0.001
	TREE_1_2	**0.130**	<0.001	**0.146**	<0.001	**0.127**	<0.001	**0.126**	<0.001	0.037	0.230	**0.212**	<0.001	**0.111**	<0.001	**0.105**	<0.001	**0.124**	<0.001
	TREE_1_10	**0.100**	<0.001	**0.147**	<0.001	**0.070**	0.002	**0.071**	0.030	0.023	0.375	**0.119**	0.006	**0.103**	<0.001	**0.140**	0.001	**0.077**	0.026
	TREE_1_100	**0.084**	<0.001	**0.143**	<0.0001	0.043	0.067	0.031	0.232	0.006	0.469	0.054	0.153	**0.094**	0.002	**0.148**	0.003	0.053	0.116
Eastern Yellow Robin	IBD	**0.052**	0.011	0.022	0.297	**0.063**	0.027	0.015	0.393	0.036	0.392	−0.005	0.518	**0.093**	0.004	0.011	0.440	**0.136**	0.014
	EO_100	**0.045**	0.037	0.008	0.419	**0.061**	0.047	0.009	0.430	0.036	0.385	−0.013	0.559	**0.068**	0.025	−0.020	0.599	**0.110**	0.033
	EO_5000	−0.019	0.603	−0.121	0.906	0.035	0.333	−0.026	0.611	0.032	0.396	−0.081	0.740	−0.098	0.869	−0.184	0.894	−0.042	0.614
	HAB_1_2	0.031	0.168	−0.013	0.590	0.056	0.106	0.005	0.462	0.075	0.287	−0.023	0.596	0.027	0.248	−0.068	0.792	0.064	0.177
	HAB_1_10	0.007	0.431	−0.049	0.755	0.048	0.219	−0.002	0.511	0.135	0.178	−0.041	0.639	−0.066	0.828	−0.158	0.909	−0.036	0.623
	TREE_1_2	0.032	0.158	−0.013	0.599	0.056	0.109	0.001	0.495	0.055	0.331	−0.025	0.605	0.028	0.257	−0.071	0.785	0.068	0.177
	TREE_1_10	0.008	0.421	−0.056	0.792	0.049	0.208	−0.015	0.560	0.091	0.251	−0.049	0.655	−0.062	0.798	−0.157	0.893	−0.025	0.583
	TREE_1_100	0.004	0.454	−0.069	0.822	0.053	0.229	−0.005	0.525	0.128	0.192	−0.038	0.611	−0.091	0.864	−0.175	0.901	−0.054	0.674
Fuscous Honeyeater	IBD	0.004	0.333	<0.001	0.494	0.006	0.323	−0.008	0.718	0.010	0.360	0.005	0.364	0.036	0.056	−0.001	0.510	0.042	0.059
	EO_5000	−0.004	0.575	−0.036	0.898	0.016	0.244	−0.002	0.525	−0.009	0.571	0.029	0.184	−0.004	0.518	−0.084	0.852	0.035	0.256
	HAB_1_10	<0.001	0.495	−0.023	0.808	0.014	0.243	−0.007	0.612	−0.003	0.536	0.017	0.272	0.012	0.372	−0.048	0.749	0.037	0.217
	TREE_1_2	0.004	0.376	−0.007	0.618	0.010	0.276	−0.012	0.720	0.005	0.442	0.002	0.460	0.037	0.121	−0.007	0.551	0.051	0.094
	TREE_1_10	0.005	0.390	−0.023	0.771	0.022	0.191	−0.010	0.622	−0.013	0.588	0.013	0.357	0.026	0.273	−0.034	0.653	0.055	0.160
	TREE_1_100	0.007	0.371	−0.037	0.851	0.035	0.115	0.003	0.456	−0.024	0.651	0.039	0.196	0.011	0.391	−0.065	0.767	0.052	0.197
Grey Shrike-thrush	IBD	**0.058**	0.042	**0.153**	0.016	**0.097**	0.045	−0.005	0.527	0.167	0.194	−0.029	0.605	0.039	0.187	0.161	0.119	0.061	0.270
	EO_100	0.056	0.051	**0.150**	0.019	0.090	0.060	−0.002	0.499	0.172	0.209	−0.027	0.594	0.029	0.265	0.162	0.134	0.038	0.362

Species		Study area						East						West					
	Sex	ALL		F		M		ALL		F		M		ALL		F		M	
	Model	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*
	EO_5000	0.020	0.352	0.105	0.072	0.007	0.445	0.025	0.350	0.170	0.242	−0.014	0.537	−0.099	0.777	0.087	0.318	−0.177	0.836
	HAB_1_2	0.046	0.108	**0.131**	0.035	0.077	0.096	0.007	0.447	0.182	0.215	−0.026	0.574	−0.002	0.498	0.139	0.188	−0.002	0.498
	HAB_1_10	0.023	0.312	0.086	0.136	0.039	0.292	0.025	0.357	0.173	0.261	−0.016	0.522	−0.078	0.774	0.074	0.352	−0.121	0.757
	TREE_1_2	0.039	0.180	**0.144**	0.037	0.044	0.253	0.013	0.421	0.160	0.267	−0.011	0.510	−0.024	0.623	0.135	0.211	−0.081	0.740
	TREE_1_10	0.002	0.479	0.114	0.123	−0.036	0.649	0.034	0.340	0.124	0.306	0.006	0.449	−0.107	0.836	0.077	0.343	−0.252	0.945
	TREE_1_100	−0.028	0.655	0.082	0.222	−0.085	0.803	0.043	0.310	0.129	0.260	−0.001	0.456	−0.147	0.895	0.029	0.435	−0.303	0.967
Superb Fairy-wren	IBD	**0.158**	<0.001	**0.111**	<0.001	**0.195**	<0.001	**0.108**	<0.001	**0.105**	<0.001	**0.102**	<0.001	**0.268**	<0.001	**0.212**	0.001	**0.323**	<0.001
	EO_100	**0.167**	<0.001	**0.109**	<0.001	**0.210**	<0.001	**0.116**	<0.001	**0.104**	<0.001	**0.118**	<0.001	**0.273**	<0.001	**0.211**	0.001	**0.329**	<0.001
	EO_5000	**0.132**	<0.001	**0.074**	0.003	**0.170**	<0.001	**0.127**	<0.001	0.054	0.107	**0.192**	<0.001	**0.205**	<0.001	0.073	0.204	**0.286**	<0.001
	HAB_1_2	**0.173**	<0.001	**0.090**	0.003	**0.231**	<0.001	**0.126**	<0.001	**0.104**	<0.001	**0.140**	<0.001	**0.251**	<0.001	**0.173**	0.005	**0.314**	<0.001
	HAB_1_10	**0.180**	<0.001	0.049	0.138	**0.257**	<0.001	**0.147**	<0.001	**0.095**	0.009	**0.194**	<0.001	**0.190**	<0.001	0.078	0.162	**0.256**	<0.001
	TREE_1_2	**0.196**	<0.001	**0.095**	0.003	**0.265**	<0.001	**0.140**	<0.001	**0.097**	0.001	**0.172**	<0.001	**0.285**	<0.001	**0.193**	0.003	**0.352**	<0.001
	TREE_1_10	**0.217**	<0.001	0.066	0.077	**0.311**	<0.001	**0.164**	<0.001	0.076	0.067	**0.240**	<0.001	**0.259**	<0.001	0.126	0.060	**0.334**	<0.001
	TREE_1_100	**0.215**	<0.001	0.046	0.199	**0.317**	<0.001	**0.168**	<0.001	0.063	0.152	**0.262**	<0.001	**0.220**	<0.001	0.071	0.211	**0.302**	<0.001
Spotted Pardalote	IBD	−0.020	0.619	0.021	0.430	−0.049	0.697	−0.060	0.935	−0.048	0.664	−0.063	0.789	0.173	0.174				
	HAB_1_2	−0.023	0.619	0.022	0.416	−0.054	0.683	−0.074	0.938	−0.050	0.639	−0.079	0.806	0.188	0.169				
	HAB_1_10	−0.019	0.575	0.021	0.425	−0.043	0.621	−0.097	0.927	−0.062	0.652	−0.091	0.782	0.212	0.201				
	TREE_1_2	−0.033	0.680	0.034	0.385	−0.083	0.777	−0.081	0.922	−0.024	0.551	−0.111	0.877	0.177	0.195				
	TREE_1_10	−0.041	0.687	0.064	0.311	−0.112	0.819	−0.096	0.856	0.029	0.392	−0.155	0.893	0.183	0.230				
	TREE_1_100	−0.032	0.626	0.091	0.264	−0.107	0.790	−0.086	0.797	0.075	0.301	−0.154	0.878	0.183	0.272				
Striated Pardalote	IBD	−0.057	0.926	−0.071	0.832	0.024	0.313	0.001	0.475	−0.109	0.853	**0.137**	0.005	−0.025	0.609	0.074	0.358	0.024	0.438
	TREE_1_2	−0.013	0.615	−0.008	0.547	0.049	0.186	0.024	0.307	−0.102	0.858	**0.126**	0.036	0.037	0.383	0.109	0.302	0.027	0.455
	TREE_1_10	0.044	0.212	0.076	0.198	0.074	0.149	0.057	0.205	−0.077	0.820	0.097	0.169	0.111	0.271	0.129	0.325	−0.003	0.509
	TREE_1_100	0.064	0.151	0.116	0.124	0.074	0.181	0.059	0.231	−0.053	0.750	0.066	0.285	0.138	0.243	0.135	0.333	−0.039	0.554
Weebill	IBD	0.013	0.302	−0.102	0.974	0.051	0.084	−0.051	0.777	−0.311	0.984	−0.007	0.549	−0.024	0.626	−0.194	0.850	−0.030	0.620
	EO_100	0.007	0.398	−0.099	0.972	0.039	0.140	−0.048	0.769	−0.311	0.982	−0.005	0.522	−0.046	0.741	−0.196	0.838	−0.070	0.750

Species		Study area						East						West					
	Sex	ALL		F		M		ALL		F		M		ALL		F		M	
	Model	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*	Mantel *r*	*P*
	EO_5000	−0.078	0.915	−0.079	0.766	−0.088	0.877	0.005	0.430	−0.291	0.982	0.051	0.267	−0.272	0.991	−0.185	0.687	−0.392	0.994
	HAB_1_2	0.001	0.462	−0.085	0.938	0.025	0.263	−0.041	0.752	−0.305	0.986	0.001	0.471	−0.088	0.857	−0.199	0.840	−0.141	0.884
	HAB_1_10	−0.026	0.682	−0.058	0.741	−0.024	0.597	−0.014	0.568	−0.274	0.991	0.023	0.321	−0.207	0.969	−0.195	0.784	−0.316	0.977
	TREE_1_2	−0.009	0.588	−0.088	0.960	0.009	0.391	−0.032	0.711	−0.284	0.987	0.007	0.411	−0.108	0.912	−0.210	0.852	−0.166	0.921
	TREE_1_10	−0.046	0.823	−0.074	0.824	−0.052	0.768	0.005	0.406	−0.222	0.989	0.038	0.251	−0.242	0.988	−0.221	0.821	−0.351	0.991
	TREE_1_100	−0.076	0.903	−0.075	0.766	−0.092	0.875	0.024	0.310	−0.174	0.976	0.052	0.240	−0.279	0.991	−0.201	0.738	−0.389	0.991
White-plumed Honeyeater	IBD	<0.001	0.490	−0.015	0.639	0.010	0.312	0.025	0.205	0.049	0.311	0.014	0.331	0.037	0.005	0.029	0.211	0.039	0.011
	EO_5000	−0.018	0.777	−0.028	0.712	−0.010	0.645	0.015	0.341	0.046	0.324	−0.006	0.543	0.001	0.486	0.036	0.280	−0.004	0.555
	HAB_1_10	−0.011	0.704	−0.015	0.630	−0.004	0.551	0.015	0.331	0.051	0.290	−0.002	0.508	0.009	0.366	0.042	0.238	0.004	0.442
	TREE_1_2	−0.011	0.689	−0.011	0.600	−0.005	0.582	0.025	0.210	0.045	0.312	0.011	0.363	0.015	0.245	0.069	0.056	0.006	0.402
	TREE_1_10	−0.023	0.797	0.003	0.487	−0.027	0.794	0.021	0.329	0.026	0.390	0.007	0.438	−0.016	0.678	0.100	0.078	−0.040	0.835
	TREE_1_100	−0.028	0.811	0.021	0.377	−0.040	0.869	0.019	0.353	0.013	0.452	0.007	0.454	−0.029	0.769	0.105	0.089	−0.058	0.903
Yellow-tufted Honeyeater	IBD	0.016	0.135	0.022	0.192	0.023	0.114	**0.049**	0.016	**0.095**	0.028	**0.063**	0.037	**0.019**	0.010	0.031	0.064	**0.023**	0.005
	EO_5000	0.016	0.228	0.015	0.314	0.020	0.236	0.038	0.103	0.019	0.360	**0.075**	0.032	0.027	0.099	**0.046**	0.037	0.024	0.181
	HAB_1_10	0.020	0.145	0.023	0.238	0.025	0.153	**0.042**	0.040	0.047	0.162	**0.077**	0.025	**0.032**	0.006	**0.049**	0.032	**0.031**	0.019
	TREE_1_2	0.025	0.068	0.032	0.129	0.031	0.075	**0.041**	0.028	0.072	0.062	**0.067**	0.034	**0.034**	0.006	**0.050**	0.034	**0.035**	0.008
	TREE_1_10	**0.039**	0.034	0.047	0.096	0.041	0.068	0.035	0.110	0.026	0.317	**0.076**	0.033	**0.053**	0.015	0.071	0.053	**0.050**	0.046
	TREE_1_100	**0.045**	0.031	0.054	0.083	0.045	0.070	0.037	0.180	−0.011	0.543	0.069	0.073	**0.059**	0.022	0.073	0.076	0.057	0.054

Appendix K. SUMMARY OF CAUSAL MODELLING FRAMEWORK RESULTS FOR F_{ST} AND INDIVIDUAL GENETIC DISTANCE

Summary of causal modelling framework results for F_{ST}. Where a single best model was selected this is listed. Where a causal modelling resulted in an indeterminate result, both IBD and the best IBR model are listed. Mantel correlation (*r*) and *P* values for test result with highest correlation, and conditioned on the highest alternative model (IBR or IBD) for each marginal and partial test are given. Supported results are in bold text.

Species	Sex	Area	N indiv	N sites	Inference	Best model(s) chosen	Marginal Mantel tests				Partial Mantel tests			
							IBD		IBR		IBD/IBR partialled out		IBR/IBD partialled out	
							r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
BT	ALL	Study		41	IBD/R	IBD/EO_100	**0.269**	<0.001	**0.263**	<0.001	0.089	0.241	−0.066	0.684
		East		15	-	-	0.124	0.124	0.221	0.109	−0.096	0.732	0.207	0.170
		West		25	IBD	IBD	**0.129**	0.024	0.123	0.076	0.041	0.428	0.016	0.422
SFW	ALL	Study		16	**IBR**	**HAB_1_10**	**0.275**	0.012	**0.567**	0.001	−0.459	0.985	**0.649**	0.004
		East		9	**IBR**	**TREE_1_100**	0.363	0.095	**0.739**	0.006	−0.161	0.697	**0.700**	0.005
		West		7	IBD/R	IBD/HAB_1_10	**0.318**	0.012	**0.610**	0.034	−0.094	0.560	0.554	0.090
YTH	ALL	Study		27	**IBR**	**TREE_1_100**	−0.022	0.597	**0.206**	0.020	−0.211	0.980	**0.290**	0.004
		East		6	-	-	−0.405	0.966	−0.018	0.418	−0.449	0.972	0.212	0.138
		West		20	**IBR**	**TREE_1_100**	−0.012	0.561	**0.340**	0.009	−0.161	0.983	**0.372**	0.009
EYR	ALL	Study		9	**IBR**	**EO_5000**	0.181	0.136	**0.732**	0.028	−0.035	0.564	0.722	0.086
		East		5	-	-	0.278	0.320	0.379	0.351	−0.279	0.783	0.380	0.190
WPH	ALL	Study		27	-	-	−0.016	0.532	−0.089	0.791	0.179	0.140	−0.199	0.886
		East		8	-	-	0.291	0.069	0.202	0.154	0.317	0.083	−0.239	0.825
		West		18	-	-	0.212	0.053	0.009	0.488	0.270	0.060	−0.171	0.785
FH	ALL	Study		25	-	-	0.069	0.115	0.230	0.058	−0.107	0.867	0.244	0.076
		East		12	-	-	0.144	0.202	0.128	0.235	0.095	0.303	−0.068	0.628
		West		12	-	-	0.038	0.355	0.179	0.174	0.009	0.474	0.176	0.175
STP	ALL	Study		8	-	-	0.305	0.095	0.312	0.124	0.037	0.484	0.080	0.397
		East		5	IBD	IBD	**0.702**	0.032	0.832	0.050	0.010	0.349	**0.628**	0.047

Summary of causal modelling framework results for individual genotypic distance. Where a causal modelling resulted in an indeterminate result, both IBD and the best IBR model are listed. Mantel correlation (*r*) and *P* values for test result with highest correlation, and conditioned on the highest alternative model (IBR or IBD) for each marginal and partial test are given. Supported results are in bold text.

Species	Sex	Area	N individuals	N sites	Inference	Best model(s) chosen	Marginal Mantel tests				Partial Mantel tests			
							IBD		IBR		IBD conditioned on IBR		IBR conditioned on IBD	
							r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
BT	ALL	Study	474	48	IBD/R	IBD/HAB_1_2	**0.142**	<0.001	**0.143**	<0.001	0.008	0.360	0.017	0.213
		East	148	19	IBD/R	IBD/EO_100	**0.147**	<0.001	**0.144**	<0.001	0.051	0.083	−0.042	0.879
		West	321	28	**IBR**	**HAB_1_10**	**0.097**	<0.001	**0.115**	<0.001	0.012	0.341	**0.064**	0.031
	F	Study	203	46	**IBR**	**EO_5000**	**0.134**	<0.001	**0.179**	<0.001	−0.010	0.615	**0.120**	0.002
		East	58	19	-	-	0.042	0.112	0.046	0.127	−0.019	0.625	0.026	0.333
		West	143	26	**IBR**	**EO_5000**	**0.062**	<0.001	**0.157**	0.001	−0.020	0.746	**0.146**	0.007
	M	Study	271	47	IBD	IBD	**0.162**	<0.001	**0.157**	<0.001	**0.077**	0.007	−0.066	0.985
		East	90	18	IBD	IBD	**0.246**	<0.001	**0.242**	<0.001	**0.099**	0.015	−0.085	0.968
		West	178	28	IBD/R	IBD/EO_100	**0.135**	<0.001	**0.135**	<0.001	0.003	0.486	0.010	0.407
EYR	ALL	Study	102	32	IBD/R	IBD/EO_100	**0.052**	0.01	**0.045**	0.033	0.062	0.120	−0.056	0.851
		East	53	15	-	-	0.015	0.405	0.009	0.441	0.069	0.164	−0.068	0.820
		West	46	16	IBD	IBD	**0.093**	0.006	**0.068**	0.028	**0.157**	0.031	−0.144	0.956
	F	Study	39	25	-	-	0.022	0.296	0.008	0.416	0.121	0.067	−0.119	0.928
		East	19	12	-	-	0.036	0.384	0.135	0.170	−0.089	0.783	0.157	0.136
		West	20	13	-	-	0.011	0.43	−0.020	0.611	0.174	0.108	−0.175	0.894
	M	Study	63	30	IBD/R	IBD/EO_100	**0.063**	0.028	**0.061**	0.048	0.023	0.388	−0.015	0.569
		East	34	14	-	-	−0.005	0.533	−0.013	0.565	0.097	0.166	−0.098	0.840
		West	26	15	IBD/R	IBD/EO_100	**0.136**	0.012	**0.110**	0.036	0.148	0.112	−0.126	0.846
FH	ALL	Study	421	33	-	-	0.004	0.329	0.007	0.374	−0.001	0.525	0.006	0.396
		East	217	14	-	-	−0.008	0.720	0.003	0.458	−0.012	0.724	0.009	0.394
		West	162	18	-	-	0.036	0.053	0.037	0.117	0.002	0.5	0.009	0.424
	F	Study	169	31	-	-	0.000	0.483	−0.007	0.610	0.031	0.226	−0.032	0.775

Species	Sex	Area	N individuals	N sites	Inference	Best model(s) chosen	Marginal Mantel tests				Partial Mantel tests			
							IBD		IBR		IBD conditioned on IBR		IBR conditioned on IBD	
							r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
		East	91	14	-	-	0.010	0.364	0.005	0.449	0.028	0.337	−0.027	0.646
		West	62	16	-	-	−0.001	0.516	−0.007	0.545	0.022	0.402	−0.023	0.602
	M	Study	252	31	-	-	0.006	0.318	0.035	0.120	−0.025	0.849	0.043	0.113
		East	126	13	-	-	0.005	0.360	0.039	0.191	−0.019	0.777	0.044	0.181
		West	100	17	-	-	0.042	0.056	0.055	0.162	0.005	0.453	0.037	0.265
GST	ALL	Study	59	32	IBD	IBD	**0.058**	0.044	0.056	0.057	0.039	0.296	−0.035	0.677
		East	26	14	-	-	−0.005	0.519	0.043	0.310	−0.039	0.714	0.057	0.277
		West	32	17	-	-	0.039	0.188	0.029	0.267	0.132	0.132	−0.129	0.859
	F	Study	23	17	IBD/R	IBD/EO_100	**0.153**	0.018	**0.150**	0.017	0.045	0.309	−0.036	0.657
		East	10	8	-	-	0.167	0.195	0.182	0.217	−0.055	0.641	0.091	0.322
		West	13	9	-	-	0.161	0.123	0.162	0.135	−0.003	0.509	0.013	0.462
	M	Study	36	26	IBD	IBD	**0.097**	0.039	0.090	0.057	0.096	0.180	−0.089	0.799
		East	16	12	-	-	−0.029	0.604	0.006	0.446	−0.053	0.679	0.045	0.365
		West	19	13	-	-	0.061	0.268	0.038	0.346	**0.254**	0.049	−0.249	0.940
SFW	ALL	Study	176	33	**IBR**	**TREE_1_10**	**0.158**	<0.001	**0.217**	<0.001	−0.019	0.710	**0.152**	<0.001
		East	108	20	**IBR**	**TREE_1_100**	**0.108**	<0.001	**0.168**	<0.001	0.007	0.438	**0.129**	0.012
		West	67	12	**IBR**	**TREE_1_2**	**0.268**	<0.001	**0.285**	<0.001	−0.010	0.565	**0.101**	0.045
	F	Study	81	29	IBD/R	IBD/EO_100	**0.111**	<0.001	**0.109**	<0.001	0.033	0.286	−0.025	0.674
		East	55	19	IBD/R	IBD/HAB_1_2	**0.105**	<0.001	**0.104**	<0.001	0.012	0.440	0.006	0.464
		West	26	10	IBD/R	IBD/EO_100	**0.212**	0.001	**0.211**	<0.001	0.027	0.391	−0.015	0.556
	M	Study	95	31	**IBR**	**TREE_1_100**	**0.195**	<0.001	**0.317**	<0.001	−0.010	0.606	**0.255**	<0.001
		East	53	18	**IBR**	**TREE_1_100**	**0.102**	<0.001	**0.262**	<0.001	−0.074	0.890	**0.252**	0.002
		West	41	12	**IBR**	**TREE_1_2**	**0.323**	<0.001	**0.352**	<0.001	−0.041	0.69	**0.153**	0.03
SPP	ALL	Study	53	19	-	-	−0.020	0.616	−0.019	0.575	−0.005	0.552	−0.004	0.507
		East	44	12	-	-	−0.060	0.930	−0.074	0.938	0.082	0.193	−0.092	0.826

Species	Sex	Area	N individuals	N sites	Inference	Best model(s) chosen	Marginal Mantel tests				Partial Mantel tests			
							IBD		IBR		IBD conditioned on IBR		IBR conditioned on IBD	
							r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
		West	8	6	-	-	0.173	0.168	0.212	0.196	−0.017	0.526	0.125	0.336
	F	Study	23	13	-	-	0.021	0.424	0.091	0.253	−0.061	0.698	0.107	0.236
		East	18	8	-	-	−0.048	0.663	0.075	0.304	−0.138	0.830	0.149	0.211
	M	Study	30	15	-	-	−0.049	0.690	−0.043	0.622	−0.023	0.628	−0.001	0.486
		East	26	11	-	-	−0.063	0.798	−0.079	0.804	0.078	0.265	−0.091	0.761
STP	ALL	Study	72	26	-	-	−0.057	0.921	0.064	0.154	−0.122	0.987	**0.125**	0.044
		East	43	15	-	-	0.001	0.474	0.059	0.227	−0.042	0.749	0.072	0.209
		West	13	8	-	-	−0.025	0.601	0.138	0.234	−0.109	0.778	0.173	0.215
	F	Study	31	18	-	-	−0.071	0.825	0.116	0.123	−0.177	0.971	**0.199**	0.047
		East	18	11	-	-	−0.109	0.856	−0.053	0.747	−0.105	0.781	0.045	0.338
		West	7	5	-	-	0.074	0.369	0.135	0.330	−0.001	0.502	0.113	0.369
	M	Study	41	21	-	-	0.024	0.320	0.074	0.148	−0.047	0.711	0.084	0.200
		East	25	12	IBD/R	IBD/TREE_1_2	**0.137**	0.007	**0.126**	0.038	0.056	0.326	−0.013	0.539
		West	6	6	-	-	0.024	0.436	0.027	0.462	0.003	0.498	0.013	0.492
WB	ALL	Study	74	24	-	-	0.013	0.297	0.007	0.379	0.094	0.101	−0.093	0.897
		East	42	13	-	-	−0.051	0.785	0.024	0.305	−0.095	0.814	0.084	0.204
		West	26	9	-	-	−0.024	0.625	−0.046	0.741	**0.266**	0.018	−0.269	0.981
	F	Study	26	15	-	-	−0.102	0.969	−0.058	0.750	−0.103	0.819	0.060	0.288
		East	14	8	-	-	−0.311	0.981	−0.174	0.974	−0.287	0.922	0.121	0.242
		West	10	5	-	-	−0.194	0.842	−0.185	0.694	−0.122	0.723	−0.107	0.453
	M	Study	48	22	-	-	0.051	0.088	0.039	0.144	**0.158**	0.032	−0.155	0.968
		East	28	12	-	-	−0.007	0.547	0.052	0.231	−0.054	0.657	0.074	0.283
		West	16	8	-	-	−0.030	0.618	−0.070	0.741	**0.405**	0.003	−0.409	0.996
WPH	ALL	Study	275	39	-	-	0.000	0.488	−0.011	0.687	0.035	0.166	−0.036	0.828
		East	76	13	-	-	0.025	0.202	0.025	0.209	0.005	0.476	0.002	0.496

Species	Sex	Area	N individuals	N sites	Inference	Best model(s) chosen	Marginal Mantel tests				Partial Mantel tests			
							IBD		IBR		IBD conditioned on IBR		IBR conditioned on IBD	
							r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
		West	192	25	IBD	IBD	**0.037**	0.004	0.015	0.237	0.055	0.081	−0.043	0.848
	F	Study	70	29	-	-	−0.015	0.636	0.021	0.372	−0.034	0.712	0.037	0.319
		East	19	8	-	-	0.049	0.308	0.051	0.284	0.003	0.487	0.013	0.468
		West	50	20	-	-	0.029	0.216	0.105	0.091	−0.010	0.580	0.101	0.125
	M	Study	205	34	-	-	0.010	0.302	−0.004	0.562	0.038	0.106	−0.037	0.872
		East	57	11	-	-	0.014	0.334	0.011	0.375	0.013	0.434	−0.010	0.544
		West	142	22	IBD	IBD	**0.039**	0.012	0.006	0.400	**0.081**	0.039	−0.071	0.927
YTH	ALL	Study	471	33	**IBR**	**TREE_1_100**	0.016	0.140	0.045	0.030	−0.019	0.843	**0.047**	0.045
		East	86	10	IBD/R	IBD/HAB_1_10	**0.049**	0.014	**0.042**	0.046	0.027	0.319	−0.013	0.575
		West	375	22	**IBR**	**TREE_1_100**	**0.019**	0.010	**0.059**	0.021	−0.013	0.796	**0.058**	0.034
	F	Study	174	30	-	-	0.022	0.199	0.054	0.083	−0.021	0.741	0.054	0.111
		East	37	8	IBD	IBD	**0.095**	0.029	0.072	0.056	**0.197**	0.022	−0.187	0.976
		West	136	21	-	-	0.031	0.064	0.073	0.071	−0.008	0.606	0.066	0.111
	M	Study	297	32	-	-	0.023	0.113	0.045	0.067	−0.010	0.654	0.040	0.128
		East	49	9	IBD/R	IBD/HAB_1_10	**0.063**	0.039	**0.077**	0.025	−0.032	0.676	0.055	0.235
		West	239	22	IBD	IBD	**0.023**	0.003	0.057	0.056	−0.007	0.634	0.053	0.093

Appendix L. NUMBER OF ALLELES PER LOCUS FOR EACH OF 10 GENOTYPED SPECIES, WITH REFERENCES FOR PRIMERS

		Species in which markers were used										
		Brown Treecreeper	Eastern Yellow Robin	Fuscous Honeyeater	Grey Shrike-thrush	Superb Fairy-wren	Spotted Pardalote	Striated Pardalote	Weebill	White-plumed Honeyeater	Yellow-tufted Honeyeater
Species and author for marker	**Locus**										
Bell Miner (*Manorina melanophrys*) (Painter et al. 1997)	BMC1			26							19
	BMC2			19						10	7
	BMC3			24	13					19	3
	BMC4			12							8
	BMC5			23							
Brown Treecreeper (*Climacteris picumnus*) (Doerr 2005)	Cpi1	17									
	Cpi2	4									
	Cpi3	6	4								
	Cpi4	5			19		21	4			
	Cpi5	8									
	Cpi6	5									
	Cpi7	5					6	16			
	Cpi8	8	4				2	4			
Domestic Chicken (*Gallus gallus domesticus*), and Zebra Finch (*Taeniopygia guttata*) (Backström et al. 2008)[1]	epic12884s2							3	5		
	epic20454s1							5			
	epic20454s2								4		
	epic23989					3					
	epic23989s				6						
	epic24254s1				4						
	epic26698s1							6	4		
	epic4550s1				7		2				
	epic6419s2						2	2			
Reed Bunting (*Emberiza schoeniclus*) (Hanotte et al. 1994)	Escmu6	13	5					19			
Pied Fycatcher (*Ficedula hypoleiica*) (Primmer et al. 1996)	FhU2			6	2	2	4	3	3	6	6
Grey Fantail (*Rhipidura albiscapa*) (Jin et al. 2006)	FT2.5				2						

		Species in which markers were used										
		Brown Treecreeper	Eastern Yellow Robin	Fuscous Honeyeater	Grey Shrike-thrush	Superb Fairy-wren	Spotted Pardalote	Striated Pardalote	Weebill	White-plumed Honeyeater	Yellow-tufted Honeyeater
Species and author for marker	**Locus**										
Barn Swallow (*Hirundo rustica*) (Primmer et al. 1995)	HrU2		7		6		4	5			2
Scottish Crossbill (*Loxia scotica*) (Piertney et al. 1998)	Lox1								1 1		
Superb Fairy-wren (*Malurus cyaneus*) (Double et al. 1997)	Mcym2					17					
	Mcym3					20					
	Mcym4					18					
	Mcym7					17			3		2
Mexican Jay (*Aphelocoma ultramarine*) (Li et al. 1997)	MJG8						4				
Song Sparrow (*Melospiza melodia*)(Jeffery et al. 2001)	Mme12									4	
Splendid Fairy-wren (*Malurus splendens melanotus*) (Webster et al. 2004)	Msp10					21					
	Msp4					10					
	Msp6					16					
Blue Tit (*Parus caeruleus*) (Dawson et al. 2000)	Pca7						15	46			
House Sparrow (Passer domesticus) (Griffith et al. 1999)	Pdo5	24			25		13				
Red-capped Robin (*Petroica goodenovii*) (Dowling et al. 2003)	Pgm1						31				
									2		
	Pgm2								6		
	Pgm3			4			3	7	3	6	
	Pgm7							3			
New Holland Honeyeater (*Phylidonyris novaehollandiae*) (Myers et al. 2009)	Pn1			6						21	29
	Pn12									6	7
	Pn13									17	24
	Pn15			4						5	
	Pn2			6							4
	Pn23			13						15	11
	Pn3										6
	Pn5			5							3
	Pn7			11						12	
Crowned Leaf Warbler (*Phylloscopus occipitalis*) (Bensch et al. 1997)	Pocc6	3	14								
	Pocc8			6							4

Magpie (*Pica pica*) (Martinez et al. 1999)	Ppi2	3			2							
		Species in which markers were used										
		Brown Treecreeper	Eastern Yellow Robin	Fuscous Honeyeater	Grey Shrike-thrush	Superb Fairy-wren	Spotted Pardalote	Striated Pardalote	Weebill	White-plumed Honeyeater	Yellow-tufted Honeyeater	
Species and author for marker	**Locus**											
	Ppm1				4							
	Ppm11				14							
	Ppm3				19							
	Ppm7				4							
	Smm2					28						
	Smm3						2	4				
									1			
	Smm6						13	13	3			
	Smm7		7	5		11	3	4		4		

[1] Primers of Backström et al. (2008) EPIC markers were redesigned (K.A. Harrison and A Pavlova unpublished data)

Appendix M. PROBABILITY OF INCLUSION OF LANDSCAPE AND SITE CONDITION VARIABLES AS PREDICTORS OF RESIDUAL BODY MASS (RBM), TOTAL BLOOD HAEMOGLOBIN (HB) AND HAEMATOCRIT (HCT)

Probability $P > 0.75$ is considered as evidence for an effect of predictor variable on a response (in bold), $P \sim 0.5$ indicates no evidence of effect (posterior probability equals prior)

Species	Response	Landscape tree cover	Landscape context (connectedness)	Landscape aggregated:continuous	Landscape aggregated:dispersed	Site canopy cover	Site shrub cover	Site log length
Brown-headed Honeyeater	RBM	0.42	0.42	0.49	0.53	0.42	0.47	0.46
	Hb	0.44	0.42	0.49	0.52	0.40	0.39	0.48
	HCT	0.46	0.38	0.50	0.46	0.43	0.39	0.38
Buff-rumped thornbill	RBM	0.43	0.43	0.51	0.50	0.45	0.43	0.47
	Hb	0.45	0.43	0.50	0.48	0.43	0.44	0.44
	HCT	0.42	0.47	0.52	0.51	0.46	0.43	0.44
Brown Treecreeper	RBM	0.40	0.41	0.49	0.49	0.68	0.35	0.41
	Hb	0.39	0.41	0.45	0.45	0.46	0.47	0.57
	HCT	0.37	0.42	0.44	0.42	0.38	0.59	0.35
Dusky Woodswallow	RBM	0.50	0.44	0.52	0.47	0.45	0.42	0.44
	Hb	0.41	0.42	0.49	0.51	0.44	0.43	0.49
	HCT	0.46	0.52	0.49	0.48	0.42	0.43	0.43
Eastern Yellow Robin	RBM	0.45	0.44	0.52	0.50	0.44	0.33	0.63
	Hb	0.45	0.47	0.46	0.49	0.49	0.44	0.40
	HCT	0.41	0.45	0.46	0.48	0.39	0.42	0.45
Fuscous Honeyeater	RBM	0.43	0.45	0.45	0.44	0.38	0.39	0.45
	Hb	0.37	0.42	0.46	0.52	0.34	0.40	0.37
	HCT	0.50	0.37	0.51	0.46	0.47	0.43	0.38
Grey Shrike-thrush	RBM	0.47	0.59	0.49	0.50	0.46	0.38	0.42
	Hb	0.54	0.39	0.56	0.53	0.39	0.42	0.41
	HCT	0.43	0.35	0.50	0.49	0.35	**0.82**	0.43
Superb Fairy-wren	RBM	0.42	0.39	0.49	0.49	0.45	0.38	0.61
	Hb	0.54	0.42	0.52	0.48	0.46	0.37	0.56
	HCT	0.44	0.46	0.50	0.47	0.43	0.49	0.49
Spotted Pardalote	RBM	0.45	0.47	0.51	0.51	0.44	0.46	0.49
	Hb	0.46	0.46	0.49	0.50	0.43	0.38	0.46
	HCT	0.45	0.44	0.52	0.48	0.40	0.41	0.63
Striated Pardalote	RBM	0.49	0.41	0.49	0.52	0.47	0.43	0.40
	Hb	0.54	0.40	0.54	0.45	0.35	0.41	0.37
	HCT	0.71	0.36	0.53	0.54	0.34	0.33	0.32
Weebill	RBM	0.43	0.45	0.46	0.49	0.42	0.43	0.51
	Hb	0.46	0.41	0.49	0.48	0.52	0.51	0.45
	HCT	0.47	0.48	0.49	0.50	0.50	0.42	0.44
White-Plumed Honeyeater	RBM	0.72	0.44	0.50	0.50	0.37	0.35	0.33
	Hb	0.35	0.44	0.51	0.58	0.34	0.34	0.42
	HCT	0.36	0.37	0.48	0.52	0.44	0.40	0.40
Yellow-tufted Honeyeater	RBM	0.40	0.39	0.47	0.51	0.47	0.39	0.42
	Hb	0.39	0.62	0.48	0.48	0.50	0.50	0.38
	HCT	0.41	0.50	0.47	0.44	0.36	0.34	0.56

Appendix N. PROBABILITY OF INCLUSION OF LANDSCAPE AND SITE CONDITION VARIABLES AS PREDICTORS OF MEAN ALLELIC RICHNESS FOR SITES WITH >5 SAMPLED INDIVIDUALS; THE SINGLE SUPPORTED RESULT IS SHOWN IN BOLD

Species	Landscape tree cover	Landscape context (connectedness)	Landscape aggregated: continuous	Landscape aggregated: dispersed	Site canopy cover	Site shrub cover	Site log length
Brown Treecreeper	0.44	0.45	0.49	0.49	0.51	0.49	0.44
Fuscous Honeyeater	0.46	0.68	0.46	0.49	**0.78**	0.36	0.39
Superb Fairy-wren	0.45	0.46	0.48	0.50	0.51	0.46	0.47
White-plumed Honeyeater	0.46	0.50	0.48	0.48	0.42	0.43	0.49
Yellow-tufted Honeyeater	0.42	0.46	0.47	0.46	0.46	0.63	0.46

Appendix O. PROBABILITY OF INCLUSION OF LANDSCAPE AND SITE CONDITION VARIABLES AS PREDICTORS OF SKEWED ADULT SEX RATIO

Species	Landscape tree cover	Landscape context (connectedness)	Landscape aggregated: continuous	Landscape aggregated: dispersed	Site canopy cover	Site shrub cover	Site log length
Brown Treecreeper	0.43	0.43	0.49	0.48	0.37	0.37	0.36
Eastern Yellow Robin	0.48	0.45	0.50	0.47	0.43	0.42	0.45
Fuscous honeyeater	0.45	0.43	0.48	0.60	0.37	0.39	0.37
Grey Shrike-thrush	0.53	0.47	0.49	0.49	0.47	0.56	0.46
Superb Fairy-wren	0.48	0.43	0.49	0.48	0.40	0.39	0.42
Spotted Pardalote	0.49	0.44	0.50	0.51	0.47	0.45	0.46
Striated Pardalote	0.44	0.47	0.47	0.50	0.39	0.40	0.40
Weebill	0.49	0.49	0.49	0.51	0.46	0.42	0.45
White-plumed Honeyeater	0.46	0.46	0.50	0.47	0.41	0.45	0.36
Yellow-tufted Honeyeater	0.43	0.66	0.45	0.54	0.47	0.36	0.32

Appendix P. PROBABILITY OF INCLUSION OF LANDSCAPE AND SITE CONDITION VARIABLES AS PREDICTORS OF HOMOZYGOSITY-BY-LOCUS (HL)

Species	Landscape tree cover	Landscape context (connectedness)	Landscape aggregated: continuous	Landscape aggregated: dispersed	Site canopy cover	Site shrub cover	Site log length
Brown Treecreeper	0.38	0.37	0.44	0.49	0.38	0.37	0.36
Eastern Yellow Robin	0.49	0.41	0.50	0.46	0.39	0.42	0.38
Fuscous honeyeater	0.41	0.40	0.49	0.44	0.35	0.37	0.40
Grey Shrike-thrush	0.46	0.37	0.49	0.46	0.40	0.42	0.60
Superb Fairy-wren	0.42	0.43	0.49	0.47	0.39	0.36	0.39
Spotted Pardalote	0.43	0.40	0.48	0.47	0.51	0.43	0.47
Striated Pardalote	0.39	0.42	0.49	0.47	0.42	0.40	0.43
Weebill	0.42	0.40	0.47	0.49	0.50	0.43	0.41
White-plumed Honeyeater	0.43	0.38	0.48	0.42	0.39	0.39	0.40
Yellow-tufted Honeyeater	0.40	0.37	0.51	0.44	0.36	0.39	0.42