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**BEYOND FRAGMENTATION:  
LIZARD DISTRIBUTION PATTERNS IN  
TWO PRODUCTION LANDSCAPES AND THEIR IMPLICATIONS  
FOR CONCEPTUAL LANDSCAPE MODELS**



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## **DECLARATION**

This thesis is my own work except where otherwise acknowledged (see Acknowledgements and Preface).

Joern Fischer

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## **PREFACE**

With the exception of Chapter 1 (Introduction) and Chapter 10 (Conclusion), this thesis is presented as a series of logically connected manuscripts, which have been published or have been submitted for publication. The content of published papers is presented as it appears in the journal acknowledged at the beginning of a given chapter, with the exception of minor stylistic changes. For example, the labelling of tables and figures was changed for consistency (e.g. Figure 1 from the paper presented in Chapter 2 was re-labelled to Figure 2.1 etc.). In all cases, the copyright of published papers is held by the journals, and permission was obtained to reproduce the papers in this thesis.

The vast majority of work on all papers was carried out by the primary author (JF), including literature searches, data collection, data analysis and manuscript write-up. However, all papers or manuscripts list other workers as co-authors to acknowledge their contributions to specific aspects of different papers. David Lindenmayer made useful contributions to all manuscripts, through helpful discussions, proof-reading, and in some cases providing data from his own work (Chapter 8, Appendices 1-3). Ann Cowling provided statistical and technical advice on the experimental design and data analysis presented in Chapters 2 and 3. Similarly, Simon Barry provided statistical advice on the analyses presented in Chapters 4 and 5. Ioan Fazey contributed to Chapters 7 and 8 by discussing important concepts with me, drafting some paragraphs of an initial version of the manuscript and proof-reading later versions. Robyn Briese contributed her legal knowledge to Chapter 7, wrote the corresponding section of an earlier version of the manuscript, and proof-read the final manuscript. Emily Flowers is listed as a co-author for Chapters 4 and 5 because she contributed several weeks of outstanding assistance in the field.

Because core chapters of this thesis are intended as stand-alone pieces of work for publication in scientific journals, some repetition between chapters was unavoidable. In addition, minor stylistic differences between chapters resulted from different journals' requirements. For example, depending on the journal a chapter was written for, chapters may begin with an "abstract" or a "summary" respectively. Similarly, although Australian

spelling is used for the vast majority of the thesis, some chapters were targeted at American journals and therefore use American English.

## ABSTRACT

Fauna conservation outside protected areas can make an important complementary contribution to conservation within reserves. This thesis aimed to contribute new information and analytical frameworks to the science of fauna conservation in human-modified landscapes. Two approaches were used: (1) empirical data collection and analysis, and (2) the discussion and development of conceptual landscape models.

Empirical work focused on lizard distribution patterns in two production landscapes in southeastern Australia. Lizards were targeted because ectotherms are frequently neglected by conservation biologists. The “Nanangroe grazing landscape” was used for sheep and cattle grazing. In this landscape, approximately 85% of pre-European woodland cover had been cleared, and understorey vegetation was sparse. Lizards were surveyed at 16 landscape units, which were stratified by aspect, topographic position and amount of tree cover. Each landscape unit contained three sites, and each site contained three plots. Regression modelling showed that different species responded differently to their environment. For example, the four-fingered skink (*Carlia tetradactyla*) and Boulenger’s skink (*Morethia boulengeri*) were more likely to occur at woodland sites with northerly aspects, whereas the striped skink (*Ctenotus robustus*) and olive legless lizard (*Delma inornata*) were more likely to inhabit sites with a simple microhabitat structure. Statistical analysis further showed that the habitat attributes that lizards were related to varied continuously through space, and over different spatial scales. For example, invertebrate abundance (a proxy for food availability) varied most strongly over tens of metres, whereas the amount of grass cover varied most strongly over hundreds to thousands of metres. Thus, work at Nanangroe revealed spatially complex patterns of lizard occurrence and habitat variables.

The “Tumut plantation landscape” was a spatial mosaic of native eucalypt (*Eucalyptus*) forest patches embedded within a plantation of the introduced radiata pine (*Pinus radiata*). In this landscape, thirty sites were surveyed for lizards. Sites were stratified by forest type and patch size, and included eucalypt patches, pine sites, and extensive areas of eucalypt forest adjacent to the plantation. Regression modelling showed that lizard species responded

to various habitat attributes, including elevation, the amount of eucalypt forest within 1 km of a site, invertebrate abundance and ground cover. Variables related to habitat fragmentation often were significant predictors of lizard occurrence. However, work at Tumut suggested that important additional insights into lizard distribution patterns could be obtained by considering variables related to food and shelter resources, and climatic conditions.

The Nanangroe and Tumut landscapes were in close proximity, but together spanned an altitudinal gradient of 900 m. An investigation of changes in lizard community composition with altitude showed that (1) only one species was common to Nanangroe and Tumut, (2) different species had different altitudinal preferences, and (3) ecologically similar species replaced one another with increasing altitude. These results highlighted that even in highly modified landscapes, natural gradients (such as climate) can play an important role in shaping animal assemblage composition and species distribution patterns.

Empirical work suggested that, in some landscapes, the frequently used “fragmentation model” is a relatively weak conceptual basis for the study of animal distribution patterns. The fragmentation model implicitly assumes that “habitat patches” can be defined unequivocally across many species, and that patches are located within a relatively inhospitable matrix. Where these assumptions are breached, conservation guidelines arising from the fragmentation model may be too simplified. In spatially complex production landscapes, it may be more appropriate to maintain habitat heterogeneity at multiple spatial scales than to focus solely on the management of large, pre-defined patches.

Given the potential limitations of the fragmentation model, a new, more holistic landscape model was developed. The “continuum model” was derived from continuum theory as developed for plant ecology. The continuum model recognises (1) spatial continua of environmental variables, and (2) species’ individualistic responses to these variables. For animals, key environmental variables may be related to the availability of food, shelter, sufficient space, and suitable climatic conditions. Unlike the fragmentation model, the continuum model is inherently process-based and thus may help to link the perceived gap between patterns and processes in landscape ecology.

Three general conclusions arise from this thesis:

1. Some heterogeneous production landscapes support many native species, and therefore represent important conservation opportunities.
2. In some modified landscapes, the fragmentation model does not capture the complexity of animal distribution patterns. In those landscapes, conservation recommendations derived from the fragmentation model may be overly simplistic.
3. The continuum model may be a useful extension of the fragmentation model. It provides a process-based conceptual basis for empirical work on animal distribution patterns.

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FIGURE A2.3. CO-OCCURRENCE PATTERNS IN THE LARGEST SITE WHERE A GIVEN TARGET SENSITIVE SPECIES WAS FOUND. PRESENCES OF CO-OCCURRING SPECIES ARE INDICATED BY A “1”, ABSENCES BY A “-”, AND “# SITES” INDICATES HOW MANY SITES A GIVEN SENSITIVE SPECIES WAS OBSERVED AT. REGARDLESS OF WHICH SENSITIVE SPECIES WAS CHOSEN AS THE TARGET SPECIES, IN THE LARGEST SITE WHERE IT OCCURRED, NO MORE THAN NINE OUT OF A POSSIBLE 20 OTHER SENSITIVE SPECIES CO-OCCURRED WITH IT. SEE APPENDIX FOR SPECIES ABBREVIATIONS. .... 241

FIGURE A3.1. SPECIES BY SITES MATRIX FOR BIRDS IN FRAGMENTS. DESPITE SUBSTANTIAL SCATTER, THE DATASET WAS HIGHLY SIGNIFICANTLY NESTED ( $p < 0.005$ ; SEE TABLE A3.1). .... 267

FIGURE A3.2. THE DATASETS FOR BIRDS IN FRAGMENTS, PINE AND “CONTROL SITES” WERE RE-ANALYSED AFTER DELETING DIFFERENT COMBINATIONS OF SITES AND SPECIES (SEE APPENDIX FOR COMPLETE LIST OF RESULTING DATASETS). EACH DATA POINT IN THIS FIGURE CORRESPONDS TO A DIFFERENT DATASET, AND INCLUDES A DIFFERENT COMBINATION OF SPECIES AND SITES. DATASETS ARE LABELLED ACCORDING TO THE SITES THEY WERE COMPRISED OF: FRAGMENTS (F), PINE SITES (P) OR “CONTROL SITES” (C). ALONG THE X-AXIS, DATASETS WERE SORTED BY THE NUMBER OF CELLS IN THE SPECIES BY SITES MATRIX. THE PLOT SHOWS HOW MANY STANDARD DEVIATIONS A GIVEN DATASET’S OBSERVED DISCREPANCY WAS BELOW THE MEAN DISCREPANCY SIMULATED BY RANDNEST. DATASETS ABOVE THE DOTTED LINE WERE SIGNIFICANTLY NESTED AT THE  $p = 0.05$  LEVEL. THE FIGURE HIGHLIGHTS: (1) LARGER DATASETS WERE MORE SIGNIFICANTLY NESTED; (2) MOST FRAGMENT DATASETS WERE NESTED; (3) FOR A GIVEN NUMBER OF CELLS IN A DATASET, THERE WAS CONSIDERABLE VARIABILITY IN THE SIGNIFICANCE LEVEL OBTAINED. .... 268

FIGURE A3.3. THE DATASET FOR BIRDS IN FRAGMENTS WAS RE-ANALYSED AFTER DELETING DIFFERENT COMBINATIONS OF SITES AND SPECIES (SEE APPENDIX). BELOW, EACH DATA POINT CORRESPONDS TO A DIFFERENT DATASET, AND INCLUDES A DIFFERENT COMBINATION OF SPECIES AND SITES. ALONG THE X-AXIS, DATASETS WERE SORTED BY THE NUMBER OF CELLS IN THE SPECIES BY SITES MATRIX. THE PLOT SHOWS HOW MANY STANDARD DEVIATIONS A GIVEN DATASET’S OBSERVED DISCREPANCY WAS BELOW THE MEAN DISCREPANCY SIMULATED BY RANDNEST. DATASETS ABOVE THE DOTTED LINE WERE SIGNIFICANTLY NESTED AT THE  $p = 0.05$  LEVEL. IN PART A, DATASETS ARE LABELLED ACCORDING TO THE SITES THEY WERE COMPRISED OF: “A” (ALL TYPES OF SITES, I.E.

HIGH ENVIRONMENTAL HETEROGENEITY) OR “VR” (*EUCALYPTUS VIMINALIS/E. RADIATA*, I.E. LOWER ENVIRONMENTAL HETEROGENEITY). IN PART B, DATASETS ARE LABELLED ACCORDING TO THE TYPES OF BIRDS THEY WERE COMPRISED OF: “S” (POTENTIALLY EXTINCTION-PRONE SPECIES), “N” (SPECIES NOT CONSIDERED EXTINCTION-PRONE), “DV” (DIVERSE COMBINATIONS OF SPECIES). IN PART C, EQUAL SIZED DATASETS WERE COMPARED: GROUP “GEN-SENS-INT” (15 SPECIES EACH, EITHER GENERALIST, SENSITIVE OR INTERMEDIATE), GROUP “HI-LO” (22 SPECIES EACH, EITHER HIGH OR LOW MOBILITY), GROUP “BIG-LIT” (30 SPECIES EACH, EITHER LARGE OR SMALL BIRDS ONLY). NO CLEAR PATTERN WAS APPARENT WITH RESPECT TO ENVIRONMENTAL HETEROGENEITY (PART A), BUT DATASETS COMPRISED SOLELY OF POTENTIALLY EXTINCTION PRONE SPECIES TENDED TO BE MORE NESTED (PARTS B AND C).....269

FIGURE A3.4. ASSESSMENT OF WHICH SPECIES WERE THE NUMERICAL DRIVERS OF NESTEDNESS IN THE BIRDS IN FRAGMENTS DATASET. IN PARTS A, B AND C, EACH DATA POINT IS A DIFFERENT BIRD SPECIES. PART A HIGHLIGHTS THAT MODERATELY WIDESPREAD SPECIES HAD THE HIGHEST ABSOLUTE DISCREPANCY. PART B SHOWS THAT UNCOMMON SPECIES HAD THE HIGHEST RELATIVE DISCREPANCY. PART C RANKS SPECIES ACCORDING TO THEIR HABITAT SPECIFICITY ALONG THE X-AXIS, AND USES LABELS FOR A SPECIES’ HABITAT SPECIFICITY FOLLOWING LINDENMAYER *ET AL.* (2003): NC (NOT CLASSIFIED), P (PINE SPECIALIST), G (GENERALIST), I (INTERMEDIATE), S (SENSITIVE). SENSITIVE SPECIES WERE OFTEN UNCOMMON IN FRAGMENTS. PART D HIGHLIGHTS THAT SENSITIVE SPECIES MAY HAVE HIGH RELATIVE DISCREPANCY VALUES (SINCE THEY WERE FREQUENTLY UNCOMMON IN FRAGMENTS).....270