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FROM PATTERN TO PROCESS: TOWARDS UNDERSTANDING DRIVERS OF DIVERSITY IN TEMPERATE WOODLANDS

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1. Using entire woodland fragments as sampling units yields data of sufficient resolution at the most appropriate scale to inform meaningful inferences and guide effective management.
2. Patch quality is paramount to long-term persistence.
3. Explicit resource-based approaches can reveal the processes underlying occurrence patterns, enabling a mechanistic understanding of the determinants of diversity in woodlands.
4. Two or three years is rarely sufficient to generate representative data on occurrence patterns of animals at patch and landscape scales.
5. Many woodland-dependent species are sufficiently mobile that targeted restoration and rehabilitation can make a real difference to their distributions. Build it and they will come.
6. Many other woodland-dependent species are dispersal-limited and strategic translocations should be considered as part of restoration efforts.
7. Fragmented landscapes are still in flux – many plants, animals and processes have not stabilised sufficiently to reflect the net consequences of habitat fragmentation over the last century.
8. The heterogeneity of nutrient inputs through space and time is crucial to sculpting the below-ground processes driving the food-webs that underpin woodland ecosystems.

Introduction

My research on temperate woodlands spans a 15-year period and includes empirical studies in *Eucalyptus*, *Acacia* and *Allocasuarina* dominated habitats in eastern Australia (see map below). I have also conducted work in various forested systems in the 'New World', and broad-based differences in the associated flora, fauna, ecological processes and history have provided

opportunities to place my emerging understanding of Australian woodlands in context and in more synthetic and generalised terms.

My current research interests fall into three broad areas: biodiversity conservation in agricultural landscapes, the biological consequences of habitat fragmentation, and ecological interactions between plants and animals. Combining community-scale descriptive work with species-specific studies, most of my work is restricted to vertebrates, although I recognise the central role that arthropod and microbial assemblages play in these systems. I have complemented this community-level descriptive approach with a resource-based experimental approach, treating mistletoe and other parasitic plants as model systems. While some of my work has been conducted in National Parks, travelling stock reserves and other public lands, most of my field sites are on private land and I work closely with natural resource agencies, regional bodies and individual landholders to convert my findings into practical on-ground outcomes.

Lessons

1. Using entire woodland fragments as sampling units yields data of sufficient resolution at the most appropriate scale to inform meaningful inferences and guide effective management

While many of the ecological processes underpinning woodland ecosystems vary at the landscape scale, the scale that defines many of the patterns within fragmented landscapes is the patch itself (Andrén 1994; Watson *et al.* 2000; Watson 2003a). Grazing regimes and other aspects of land use; fire frequency and other disturbances vary primarily at the patch scale and, while moderated by within-patch heterogeneity, it is often patch-scale factors that ultimately determine whether or not particular species occur within a habitat fragment (Ewers and Didham 2006). Yet the way most patchy landscapes are studied is using fixed-effort methods applied within patches – quadrats, transects and plots of fixed areas arranged in woodland fragments and the surrounding matrix (e.g. Mac Nally and Watson 2007). While useful from a statistical standpoint and the basis of rigorous comparisons, resultant data can be misleading – even nonsensical – and can obfuscate the underlying patterns. Thus using a fixed area transect to measure tree density in a woodland patch misses the point – organisms occurring within this woodland are not influenced by any single value: they are responding to the variation in structure and composition of trees within the entire patch. Likewise, a particular species of lizard is not influenced by the presence or absence of a particular substrate within a randomly placed quadrat, but responds to the density of this substrate within the entire patch (Watson and Peterson 1999; Watson 2003b).

This approach also extends to animal sampling: if the key question hinges on species-richness estimates in habitat patches, it is counter-intuitive to exclude those species seen within the patch that happened to be detected outside the transect boundaries during sampling. Various approaches can be used to design sampling regimes at the patch scale, including the use of results-based stopping rules to ensure samples from patches of differing size and quality are of equivalent completeness (Watson 2003a). Most importantly, patch-scale data yields information at the most relevant scale for land managers. Grazing regimes and fire frequencies are not applied at the quadrat or transect scale, but to the entire patch. Hence, not only do patch-scale data represent reality better, they give managers the information essential to set meaningful targets and achieve real on-ground improvements. When interpreting the findings of studies conducted using fixed-effort sampling methods at smaller scales, the reader should be careful not to extrapolate the data up to the patch scale: even though a species was not recorded within the sampling area, it still may reside in the patch.

2. Patch quality is paramount to long-term persistence

'Location' is frequently touted as all-important, whether by estate agents selling a house, conservation agencies justifying their actions or landscape ecologists interpreting their data. Position in the landscape, proximity to putative corridors, distance from presumed source areas are all key criteria driving the way we consider and manage populations of plants and animals in woodland remnants and other fragmented systems. Studies from older systems – hundreds and thousands of generations after fragmentation – paint a very different picture (Watson 2002a; Ewers and Didham 2006; Watson 2009). Isolation, connectivity and other landscape-scale measures are invariably eclipsed by measures of patch quality: the bigger fragments containing the better habitats and the wider range of microhabitats retain more species. Thus if we are concerned about long-term persistence of local populations and averting extinctions of species now restricted to fragmented systems, we must apply these lessons from older systems and strive to retain and restore the largest and most intact habitats remaining. Bigger patches necessarily contain a wider range of landforms and associated soil types and habitats, yet even the largest fragments may not be large enough – thresholds for persistence in some systems extend into the thousands of hectares (Watson 2003a). As well as validating the large-scale connectivity and restoration initiatives presently underway in Australian woodlands, this realisation calls into question most of the investment of regional and local agencies in small-scale revegetation and rehabilitation.

3. Explicit resource-based approaches can reveal the processes underlying occurrence patterns, enabling a mechanistic understanding of the determinants of diversity in woodlands

One shortcoming with patch and landscape-based approaches is that the measured variables rarely influence individual organisms directly – ravens (*Corvus spp.*) do not selectively predate nests in smaller fragments, nor do Greater Gliders (*Petauroides volans*) prefer trees growing in larger patches. Rather, individual animals respond directly to particular resources – food, shelter, cover from predators. These responses are typically directional, rapid, and predictable (i.e. nest predators prefer sites with higher nest densities, arboreal folivores avoid sites with insufficient hollows; Andren 1994; Lindenmayer 1997; Gibbons and Lindenmayer 2002). By studying distribution patterns of organisms relative to availability of carefully selected resources, not only can direct patterns of dependence be revealed, but indirect interactions with patch and landscape-scale factors can be discerned (i.e. larger patches typically support a greater size range of trees, thereby explaining why gliders occur frequently in larger patches). In addition to yielding more meaningful inferences, resource-based approaches provide testable predictions and concrete targets ideally suited to adaptive management techniques (Watson 2001; Watson and Herring 2006).

4. Two or three years is rarely sufficient to generate representative data on occurrence patterns of animals at patch and landscape scales

Two of the climatic factors that define temperate woodlands – inherently low rainfall and high variation in annual rainfall – mean that any one season is not representative of actual occurrence patterns (Maron *et al.* 2005). The summary statistics typically used to characterise ecosystems (long term averages of temperature, rainfall, number of frosts, etc.) have little meaning. Rather it is the variation in these parameters and the occasional extreme event that matter more: defining range limits, constraining distributions and explaining timing of reproduction (Stevens and Watson 2006; Barea and Watson 2007). The best way to quantify this variation and discern signal from noise is to move beyond the standard two or three-year study – periods which are simply not long enough to gain a representative sample of many patterns and processes (Watson 2009). This approach need not involve continuous monitoring. Single samples every spring for five years may be far more informative than three continuous years of sampling for many questions in many regions, despite requiring a fraction of the resources. Researchers need to be creative about designing studies to maximise their temporal relevance, and funding bodies and policy makers need to be far more realistic in the level of investment directed towards empirical research. Short-term studies of landscapes yield many answers and most of them are wrong (Strayer *et al* 1986, Stohlgren *et al.* 1995).

5 Many woodland-dependent species are sufficiently mobile that targeted restoration and rehabilitation can make a real difference to their distributions. Build it and they will come

Some woodland-dependent plants and animals are highly mobile, able to move long distances to find suitable conditions or required resources (Watson *et al.* 2000). Given inherent variation in resource availability (whether water, nectar, insects or rodents), many woodland species are readily able to travel long distances – often through relatively inhospitable habitat – buffering populations against local shortages and short-terms periods of scarcity. This is most clearly demonstrated by birds and bats, two diverse groups that contain many woodland-dependent species. Studies from isolated remnants and longer-term studies measuring inter-annual variation across multiple sites have documented high levels of species turnover in these groups (e.g.

Maron *et al.* 2005). This dynamism is driven by the comings and goings of species, prospecting across the landscape looking for particular resources. While this has previously been considered in terms of demographic and genetic consequences for species persistence in relictual landscapes, the inherent mobility of many woodland species also has important implications for revegetation and restoration initiatives. Although adding to existing remnants will always be preferable, revegetation plots in greenfield sites are visited by a large number of woodland species. If the new patch is big enough and contains sufficient resources, these visitors will stay for longer and may even breed. As well as providing recruits to arrest declining populations, the status of revegetated plots as habitat represents a much-needed success story– just the sort of thing needed to inspire landholders and management agencies to maintain their motivation and continue their efforts.

6. Many other woodland-dependent species are dispersal-limited and strategic translocations should be considered as part of restoration efforts

Although many woodland species are sufficiently mobile to colonise new or improved patches, many species are not and are effectively marooned in habitat remnants. Whether unable to move long distances or subject to predation outside woodland habitats, many reptiles, amphibians and small mammals can become stranded. This has two consequences. Firstly, those woodland remnants where a species persists soon contain more individuals than can be supported, leading to increased levels of density-dependent mortality and greater likelihood of local extinction. Secondly, once the population of a particular species has gone extinct within a particular patch, the woodland is unlikely to be recolonised in the future, even though it may contain all the resources needed by that species. So, for a particular species in a given landscape, there may be too many individuals in some patches of decreasing quality and no individuals in patches of increasing quality. A short-term solution to this situation is targeted translocations– moving individual animals to unoccupied patches. Rather than willy-nilly, these actions would need to be carried out in an informed and carefully monitored manner (Vitt *et al.* 2009). The Landcare movement has demonstrated the great willingness of landholders to repopulate their production-dominated properties with the plants that used to occur there – why not give them the opportunity to put some of the animals back as well?

7. Fragmented landscapes are still in flux – many plants, animals and processes have not stabilised sufficiently to reflect the net consequences of habitat fragmentation over the last century

Most fragmented woodlands in southern Australia are the result of widespread clearing for agriculture that occurred 80–120 years ago. While this may seem ample time for various groups of organisms to have adjusted, consider this time period relative to the taxa that comprise this habitat. The various tree species that define these woodlands typically take decades to attain reproductive maturity and a century or more to acquire the hollows necessary for many woodland-dependent animals. As such, the time since fragmentation in most temperate woodlands represents less than one cohort of these plants and the effects of initial clearing and subsequent perturbation on the regeneration and overall structure of the habitat are yet to be fully realised (Watson 2003b). Recognising the age of the landscapes being studied relative to the organisms and processes being studied is critical (Watson 2002b) – the woodland fragment that has supported two generations of trees and 10 generations of cicadas feeding on their sap has also yielded more than 50 generations of *Antechinus* and hundreds of generations of the isopods they eat. Rather than choose the organism before the question, it is far more meaningful to select the question of interest, consider the appropriate time frame and then study the organism best suited to revealing changes over that duration.

8. The heterogeneity of nutrient inputs through space and time is crucial to sculpting the below-ground processes driving the food-webs that underpin woodland ecosystems

All organisms ultimately depend on water and nutrients, yet the importance of nutrient availability in explaining occurrence patterns of plants, animals and fungi in fragmented landscapes has only recently emerged and has yet to be fully appreciated in temperate woodlands. The nitrogen-fixing trees and shrubs that originally provided most of the soil-borne nitrates have undergone dramatic changes in abundance. Some were cleared, others actively promoted for commercial purposes (e.g. wattle bark for tanning leather) and most are preferentially consumed by domestic stock. The soils that have some of the lowest available phosphorous on earth require large and frequent inputs to grow food and fibre, with surface run-off and spray drift dramatically elevating levels in adjacent woodlands. The mistletoes and parasitic shrubs that concentrate nitrogen, phosphorous and various micronutrients have undergone marked changes in abundance, becoming super-abundant in some regions, locally extinct in others (March and Watson 2007). Finally, fire regimes in these woodlands have drastically changed, typically becoming less frequent and more intense, increasing or decreasing availability of some elements by orders of magnitude. Applying findings of similar patterns described in other ecosystems (Harris 2009), these changes to nutrient inputs have likely driven dramatic changes in the below-ground microbial community, altering their composition and thereby fundamentally modifying the foundation of woodland food-webs. Understanding these changes, following them through food webs and investigating the potential to restore the structure and function of microbial assemblages are key goals for woodland biologists, and new collaborations with other groups of biologists are needed to apply this bottom–up approach.

Conclusions

When considering woodlands, the starting position for most managers, policy makers and landholders is the status quo: current habitats provide a reliable indication of their original composition and represent templates for restoration and long-term preservation. This steady-state mentality is at odds with a growing understanding of how woodlands function and how ecological processes within them have changed over the last century. Species come and go, disturbances and other rare events have a disproportionate effect on community composition and changes in surrounding habitats entrain dramatic changes within remnants. Acknowledging these sources of variation and the extended time frames within which they operate is essential, both to interpret existing studies of these systems, but also to design new studies to fill critical knowledge gaps.

Most of our woodlands are gone, and most of the remainder have been greatly modified, yet we have lost surprisingly few species. While noting that the full repercussions of our actions are yet to run their course, this demonstrates the great resilience of these ecosystems and suggests that populations and processes may rebound if we make the right decisions. Applying the lessons learned, investing in ongoing research, rewarding sound land management and keeping our eyes on longer term targets, I am confident we can safeguard the long-term functionality of our temperate woodlands.

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Bio

Dave Watson completed a Bachelor of Science at Monash University before conducting his Honours research on fragmented Buloke woodlands with Ralph Mac Nally and Andrew Bennett. His PhD at The University of Kansas examined the long-term effects of habitat fragmentation using case studies of highland birds in Mesoamerica. He returned to Australia in 1999, taking up a position at Charles Sturt University where he is now Associate Professor in Ecology. He lives with his family on a rural property near Albury, which is slowly being transformed from degraded farmland to grassy-box woodland.

References

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–366.

Barea, L. and Watson, D.M. (2007). Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. *Emu* **107**, 203–209.

Ewers, R.M. and Didham, R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* **81**, 117–142.

Gibbons, P. and Lindenmayer D. (2002). *Tree hollows and wildlife conservation in Australia*. CSIRO.

Harris, J. (2009). Soil microbial communities and restoration ecology: facilitators or followers? *Science* **325**, 573–576.

Lindenmayer, D.B. (1997). Differences in the biology and ecology of arboreal marsupials in forests of Southeastern Australia. *Journal of Mammalogy* **78**, 1117–1127.

Mac Nally, R.C. and Watson, D.M. (1997). How does habitat-island area affect species richness? Birds in Victorian Buloke remnants. *Austral Ecology* **22**, 227–232.

March, W.A. and Watson, D.M. (2007). Parasites boost productivity: effects of mistletoe on litter dynamics in a temperate Australian forest. *Oecologia* **154**, 339–347.

Maron, M., Lill, A., Watson, D.M., Mac Nally, R. (2005). Temporal variation in bird assemblages: how representative is a one-year snapshot? *Austral Ecology* **30**, 383–394.

Stevens, H.C. and Watson, D.M. (2006). Effect of rainfall on breeding of grey shrike-thrushes *Colluricincla harmonica*. *Corella* **30**, 16–20.

Stohlgren, T.J., Binkley, D., Veblen, T.T. and Baker, W.L. (1995). Attributes of reliable long-term landscape-scale studies: malpractice insurance for landscape ecologists. *Environmental Monitoring and Assessment* **36**, 1–25.

Strayer, D, Glitzenstein, J.S., Jones, C.G., Kolasa, J., Likens, G.E., McDonnell, M.J., Parker, G.G., Pickett, S.T.A. (1986). Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. *Occasional Publication of the Institute of Ecosystem Studies* **2**, 1–38.

Vitt, P., Havens, K. and Hoegh-Guldberg, O. (2009). Assisted migration: part of an integrated conservation strategy. *Trends in Ecology and Evolution* **24**, 473–474.

Watson, D.M. (2009). Continental Islands. In *Encyclopaedia of Islands*. (Eds R. Gillespie and D. Clague). University of California Press: Berkeley.

Watson, D.M. (2003a). The 'standardized search': an improved way to conduct bird surveys. *Austral Ecology* **28**, 515–525.

Watson, D.M. (2003b). Long-term consequences of habitat fragmentation: highland birds in Oaxaca, Mexico. *Biological Conservation* **111**, 283–303.

Watson, D.M. (2002a). A conceptual framework for the study of species composition in islands, fragments and other patchy habitats. *Journal of Biogeography* **29**, 823–834.

Watson, D.M. (2001) Mistletoe – a keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics* **32**, 219–249.

Watson, D.M. and Herring, M. (2006). Of mistletoe and mechanisms – drivers of declining biodiversity in remnant woodklands. *Proceedings of Veg Futures Conference*: 1–7.

Watson, D.M., Mac Nally, R.C. and Bennett, A.F. (2000). The avifauna of remnant Buloke (*Allocasuarina luehmanni*) woodlands in western Victoria. *Pacific Conservation Biology* **6**, 46–60.

Watson, D.M. and Peterson, A.T. (1999). Determinants of diversity in a naturally fragmented landscape: bird faunas of humid montane forests in Mesoamerica. *Ecography* **22**, 582–589.