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Running Head: Theory in ecology and conservation

Framework to improve the application of theory in ecology and conservation

Don A. Driscoll

David B. Lindenmayer

Fenner School of Environment and Society
The Australian National University
Canberra ACT 0200

email:
don.driscoll@anu.edu.au
david.lindenmayer@anu.edu.au

Abstract. Ecological theory often fails applied ecologists in three ways: (1) theory has little predictive value but is nevertheless applied in conservation with a risk of perverse outcomes; (2) individual theories have limited heuristic value for planning and framing research because they are narrowly focused and; (3) theory can lead to poor communication among scientists and hinder scientific progress through inconsistent use of terms and widespread redundancy. New approaches are therefore needed that improve the distillation, communication and application of ecological theory. We advocate three approaches to resolve these problems: (1) improve prediction by reviewing theory across case-studies to develop contingent theory where possible; (2) plan new research using a checklist of phenomena to avoid the narrow heuristic value of individual theories; (3) improve communication among scientists by rationalizing theory associated with particular phenomena to purge redundancy and by developing definitions for key terms. We explore the extent to which these problems and solutions have featured in two case studies of long-term ecological research programs in forests and plantations of south eastern Australia. We find that our main contentions are supported regarding the prediction, planning and communication limitations of ecological theory. We illustrate how inappropriate application of theory can be overcome or avoided by investment in boundary-spanning actions. The case studies also demonstrate how some of our proposed solutions could work, particularly the use of theory in secondary case studies after developing primary case studies without theory. When properly coordinated and implemented through a widely agreed upon and broadly respected international collaboration, the framework that we present will help to speed the progress of ecological research and lead to better conservation decisions.

Key words: *disturbance theory; heuristics; island biogeography; metacommunity; metapopulation; research planning; science communication; Tumut Fragmentation Study; unified theory; Victorian Mountain Ash forest*

INTRODUCTION

The field of conservation biology presents a contradiction in the way it uses ecological theory. On one hand, theory is deeply embedded within the field, and is applied directly or indirectly in conservation decision-making (Doak and Mills 1994, Simberloff 1998). On the other hand, most papers published in conservation journals make little or no use of theory (With 1997, Fazey et al. 2005). Ecological theory is being used for making resource-management decisions, but applied ecologists most often report research as though theory does not exist.

We believe this is a problem. If few applied ecologists work to develop theory, then the theory used for supporting decision-making will improve at a slow pace, if at all. However, improvement is needed because application of contemporary ecological theory can lead to detrimental management outcomes (Shrader-Frechette and McCoy 1993, Doak and Mills 1994, Harrison 1994). Further, accelerated progress is demanded as the conservation challenges facing land managers continue to increase. Decisions must be made in the context of the global biodiversity crisis (Koh et al. 2004, Stork 2010), made worse by climate change and increasing demand for resources (Ayres 2000, Butchart et al. 2010). For ecologists to provide information and guidance at the pace demanded, we first need to have theory that can make reasonable predictions about the consequences of management interventions. We also need to be able to plan and frame research that addresses the most important conservation and ecological questions, and we need to communicate our research results to one another effectively.

Ecological theory has the potential to support these needs for prediction, research planning, and communication among scientists. But how well does theory perform in each of these roles and where does it fail? We present three challenging answers. We contend that, currently, theory often fails in prediction because the spatial, temporal and taxonomic circumstances in which a theory applies are often not defined and this failure of prediction can lead to perverse management outcomes. We show that theory can often have limited research-planning value because individual theories span a narrow range of concepts. Finally, we argue the proliferation of theory limits communication among scientists and hinders scientific progress because terms are poorly defined, and because much theory is redundant. To address these weaknesses, we present specific suggestions that build on the concept of integration of ecological theory (Pickett et al. 1994) and is aimed at improving the way theory is used in applied ecology (Table 1, Fig. 1). We then challenge our arguments about the limitations of theory using two long-term research programs. These case studies provide direct evidence that the way theory is currently used can limit research progress, but they also illustrate some of the possible solutions. We argue that, ultimately, the framework we present will improve the use of ecological theory in conservation, supporting more rapid accumulation of knowledge. Combined with improved cross-boundary communication, ecologists will be better able to promote informed conservation management.

THEORY - DEFINITION

Different terminology and emphases are used by different authors to define theory (c.f. Pickett et al. 1994, Ford 2000). A discussion of definitions of theory is not one of our goals, but we agree with Pickett et al (2004) that theory is a system of conceptual constructs. Pickett et al. (1994) and Ford (2000) emphasised that such systems consist of several components including axioms or assumptions, hypotheses (testable statements), and concepts (labeled phenomena). The simplest form of a theory therefore consists of a testable hypothesis, and the associated assumptions and concepts, although such a theory may be nested within a larger body of theory.

PREDICTION

When supported by empirical evidence, theory can predict ecological change and support management decisions. For example, incidence function models based on metapopulation theory can predict patterns of landscape occupancy and change for well-studied species (Hanski et al. 1996). The British butterfly *Hesperia comma* exhibits population structure and dynamics that satisfy the main assumptions of metapopulation theory (Thomas et al. 1986, Hill et al. 1996). On this basis, Wilson et al. (2009) were able to apply a metapopulation model, with parameters estimated using data from a landscape of over 100 sites. In three of four test landscapes, the predicted changes in distribution over 18 years were well matched with the observations. Similarly, a patch-occupancy model for the Florida scrub lizard (*Sceloporus woodi*) developed in one landscape was able to accurately predict patch occupancy in two test landscapes (Hokit et al. 1999). When a predictive capacity has been proven for a species, metapopulation models can be used to rank management alternatives for improving landscape connectivity and reducing the risk of metapopulation extinction (Drechsler et al. 2003, Nicholson and Possingham 2007, Wilson et al. 2010).

In contrast with empirically verified, **local** application of theory, substantial evidence spanning two decades demonstrates that ecological theory has very limited **general** predictive capacity (Peters 1991, Shrader-Frechette and McCoy 1993, Caughley 1994, Doak and Mills 1994, Schemske et al. 1994, Lawton 1999). Earlier critics (Shrader-Frechette and McCoy 1993, Doak and Mills 1994) focused on metapopulation and island biogeography theories, demonstrating that the idiosyncrasies of particular ecological systems made prediction unreliable. Other popular ecological theories suffer from similar weaknesses. For example, although there is some evidence supporting the intermediate disturbance hypothesis, most cases do not support predictions of higher diversity at medium disturbance levels (Mackey and Currie 2001). Similarly, edge effects that include elevated nest predation or parasitism have been observed in north-western Europe and parts of North America, but predictions often do not hold in Central Europe, Central America, Australia and many tropical landscapes (Lahti 2001, Batary and Baldi 2004, Ries et al. 2004, Hausmann et al. 2005, Lindenmayer and Fischer 2006). We have recently examined the application of assembly rules, metacommunity and metapopulation theory and found that these common theories had no, or very little predictive value in a series of case studies (Driscoll 2008, Driscoll and Lindenmayer 2009, Driscoll et al. 2010, Driscoll and Lindenmayer 2010). As a final example, general predictions about conservation management have emerged from demographic theory (Sinclair 1996) but species-level idiosyncrasies and temporal variation have made predictions weak. Attempts to link mammal population growth with age of first female reproduction (Hone et al. 2010) indicated extremely wide confidence limits due to species-specific responses. Additional uncertainty arose from temporal variation in age of first reproduction (Hone et al. 2010). Hone et al. (2010) warn that a case-by-case evaluation of precision is needed. Our point here is that if theory is applied to new situations for which there is no relevant empirical data, the literature suggests that more often than not, theory will fail to describe that new system.

Despite ecological theory lacking general predictive capacity, theory is frequently applied in conservation and land management with the implicit assumption that predictions from theory provide a reasonable guide for management. For example, assumptions about connectivity, metapopulation dynamics, and patch-matrix landscapes are common in tools for landscape planning (Hersperger 2006, Termorshuizen et al. 2007) and reserve design (Nicholson et al. 2006, Edwards et al. 2010). Ecological theory underlies many scenario-planning approaches in ecology (Cumming 2007), and these are widely applied in environmental planning (Palomo et al. 2011). Theory has also been applied directly to support, for example, biodiversity management strategies based on keystone, indicator or ecosystem-process theories (Simberloff 1998), networks of small reserves based on metapopulation theory (as discussed by Harrison 1994), and corridor construction arising from fragmentation theory (Russell 1994).

With weak predictive capacity, the application of theory in conservation can lead to management mistakes. For example, in north-western USA, forest logging options were identified on the basis of population viability analysis (PVA) of the Northern spotted owl *Strix occidentalis caurina* (Harrison 1994). Subsequent scrutiny of the models in court revealed the metapopulation assumptions of the PVA were poorly supported. Management based on theory was deemed to be a substantial threat to the Northern spotted owl (Harrison 1994). Other examples of the potential for management mistakes include; metapopulation theory applied to captive populations of Puerto Rican Parrots *Amazona vittata* (Lacy et al. 1989, Wilson et al. 1994), patch-matrix assumptions applied in managing boreal forest birds (Schmiegelow and Monkkonen 2002), indicator species concepts applied in forest management (Simberloff 1998, Lindenmayer and Likens 2011), the intermediate disturbance hypothesis applied to fire management in an

Australian national park (Lindenmayer et al. 2008d, Lindenmayer et al. 2008e), and landscape-planning tools used for predicting the distribution of small mammal habitat (Corry and Nassauer 2005). Given the pervasive use of theory in conservation and the potential for management mistakes, there is substantial motivation for applied ecologists to use theory more effectively.

RESEARCH PLANNING AND FRAMING

The early critics of applying theory in conservation and ecology nevertheless emphasised that theory is still valuable because it provides important conceptual frameworks to motivate and guide research (Shrader-Frechette and McCoy 1993, Doak and Mills 1994, Schemske et al. 1994). Metapopulation theory is a good example (Doak and Mills 1994, Krohne 1997, Esler 2000, Driscoll 2007). Even though a species may not conform to a particular type of metapopulation, effective species management depends on understanding the processes that are highlighted by metapopulation theory such as dispersal and persistence of local populations (Hanski 1999, Hanski and Gaggiotti 2004). Research addressing the questions that arise from metapopulation theory will lead to new knowledge that better identifies theory relevant to a given system, and contributes general insight into how common particular phenomena might be (Driscoll 2007). By investigating one theory, a researcher may learn that alternative theories are more likely to apply. An important role of theory is therefore to alert the researcher to the range of possible ecological phenomena, to guide the formulation of research questions about the most important processes or patterns, and to help structure learning such as through rejection of initial theories and elaboration of alternatives.

This planning and framing function of theory has a negative side. With a pivotal role in setting up research questions, theory can constrain the design of experiments, limiting the scope of questions that are asked and the approaches that are taken. For example, Haila (2002) argued that the popularity of island biogeography theory constrained much research to questions about the influence of patch size on species richness, but these questions often have limited relevance in conservation. Working within the conceptual domain of island biogeography prevented a focus on other questions that are important for conservation, particularly about how species use the matrix, habitat loss, fragmentation and causes of extinction (Haila 2002). Similarly, the patch-matrix assumption of metapopulation theory leads to a focus on presence or absence of a species in the matrix. However, in many landscapes, there may be a continuum of landscape use (Austin 1999a, Fischer and Lindenmayer 2006). Using a patch-matrix model, conservation attention is directed towards creating habitat patches and connections, whereas in some systems it is possible that more substantial conservation gains could be made by altering the "matrix" (Franklin 1993, Fahrig 2001, Fischer and Lindenmayer 2006), by increasing the total amount of habitat (Schmiegelow and Monkkonen 2002, Fahrig 2003), or improving patch condition (Harrison and Bruna 1999).

The narrow conceptual domain of theory can slow the rate of knowledge acquisition. For example, edge effects theory emphasizes interactions between species at the boundary of adjacent vegetation types, and much research has focussed on how predator-prey interactions are influenced by the nature of the edge (Paton 1994, Lahti 2001, Sisk 2007). However, in a review of predator-prey theory, Ryall and Fahrig (2006) argued that faster progress in understanding interactions between predators and their prey in patchy landscapes required a landscape scale approach. The popularity of edge theory, combined with its emphasis on the patch scale, may have slowed progress in the field by directing much research towards questions that were not the most important for understanding the phenomenon (Ryall and Fahrig 2006). More rapid research progress is therefore likely when a broad conceptual framework is used for guiding and interpreting research rather than a narrow focus on particular theory.

COMMUNICATION AMONG SCIENTISTS

While theory can fail in its predictive and planning roles at the beginning of the research cycle, theory should nevertheless be useful towards the end of the cycle as a communications tool. The practicalities of communicating with an international scientific audience demand that a common set of terms is available for describing particular phenomena. Researchers who study different taxonomic groups on opposite sides of the globe can nevertheless find common ground through shared concepts and in practice, through literature searches for shared key-words associated with a particular theory (e.g. Akcakaya et al. 2004, Ranius 2007). Given the potential explanatory value of theory in particular case-studies, theory could provide an essential set of concepts that facilitate effective communication. For example, metapopulation theory includes a well defined set of metapopulation types based on variation in extinction risk, dispersal rate, the rate of extinction relative to colonization and the cause of extinctions (stochastic or deterministic) (Harrison and Taylor 1997, Hanski 1999, Driscoll 2007). After gathering evidence about a study system using a metapopulation approach, the kind of metapopulation dynamics that the system displays can be readily communicated to a wide audience (e.g. Dunham and Rieman 1999). Interpreting case studies in terms of popular theory is therefore like translating the study into an international language; it enables studies that report similar phenomena to be readily identified and linked, with the potential for synthesis of the circumstances in which those phenomena are important.

Although theory has the potential to enhance progress by increasing the efficiency and extent of knowledge transfer between researchers, there are two key barriers undermining this ideal. First, effective communication can be confounded by poorly defined terms or conflicting definitions (Peters 1991, Shrader-Frechette and McCoy 1993, Hall et al. 1997). For example, fragmentation is one of the most widely applied concepts in conservation (Fazey et al. 2005) but poor definition of terms (e.g. "habitat") and domain (e.g. amount, condition, isolation and breaking apart of habitat) has led to substantial confusion (Fahrig 2003, Lindenmayer and Fischer 2007). Similarly, the indicator species approach can refer to using particular taxa as surrogates for environmental change (Landres et al. 1988), but can also simply refer to the species that is measured without assuming that the species provides additional insight into the state of the ecosystem (Woodward et al. 1999, Heink and Kowarik 2010). With multiple meanings, it is difficult to communicate particular effects and this has substantial, practical consequences. Confused application of terms inhibits knowledge development and sharing, promotes unproductive debate, and prevents effective mitigation of threatening processes (Lindenmayer and Fischer 2007, Lindenmayer and Likens 2011), with the potential for major errors in resource management (Shrader-Frechette and McCoy 1993). Although poorly defined terms are inevitable as new fields expand (Hodges 2008), much ecological theory and the associated terms are in need of clarification (see the many papers cited in WebTable 1 of Hodges 2008).

A second reason that theory struggles to serve an ideal communications role is that there can be multiple theories that describe the same phenomenon (Austin 1999b). Different streams of theory can develop in isolated "ivory publishing towers", insulated by separate sets of key-words and particular applications. For example, the process of net movement of organisms from one region to another is described by at least six separate theories: mass-effects metacommunity theory (Shmida and Ellner 1984, Shmida and Wilson 1985, Leibold et al. 2004), spill-over edge effects (Rand et al. 2006), spatial subsidies (Polis et al. 1997), source-sink effects (Pulliam 1988), rescue-effects (Brown and Kodric-Brown 1977) and mainland-island metapopulation theory (Harrison 1991). Despite substantial conceptual overlap, some of these theories have limited overlap in the literature. Since 1997, 52 papers have cited the key spatial subsidies paper by Polis *et al.* (1997) and mention spatial subsidies in the abstract or key words. Of these, two papers cited one of the key mass-effects papers (Shmida and Ellner 1984, Shmida and Wilson 1985), two cited Leibold *et al.* (2004) and three mentioned metacommunities. Conversely, 33 papers have cited the key mass-effects papers (Shmida and Ellner 1984, Shmida and Wilson 1985) since 1997 and also mention mass effects in their abstract or key words. One of these papers also cites Polis *et al.* (1997). We acknowledge that each theory includes different nuances (e.g. source-sink effects and rescue-effects imply that the sink is not a self-sustaining population while the others do not necessarily imply that; spatial subsidies imply mass movement of any resource whereas mass effects refers only to organisms). Nevertheless, any one theory could be readily adapted to cover the entire suite of nuances, delivering a set of terms that can be shared more widely across case-studies.

Redundancy in theory is widespread. Other examples of redundancy can be found in the overlap of island biogeography, metacommunity, metapopulation and nested subset theory (Driscoll 2007, 2008, Simberloff and Collins 2010), keystone theory and a suite of redundant alternative terms (transformers, foundations, engineers, dominants, Simberloff 2004), r-K life history strategies (Southwood 1977), unified theories in macroecology (McGill 2010), habitat heterogeneity / disturbance theory (Huston 1979) and ecological stability concepts, where Grimm and Wissel (1997) identified 163 definitions for 70 different stability terms, when there are only six different stability phenomena (Grimm and Wissel 1997).

Research progress is slowed when ecologists are divided by redundant theory. In their classic paper on succession theory, Connell and Slatyer (1977) described a succession where earlier colonists of recently disturbed sites (good dispersers) were replaced by late-arriving stronger competitors (poor dispersers). Connell and Slatyer (1977) suggested there was very little evidence for this "tolerance" model of succession. However, there were many examples of this phenomenon in the published literature by the mid-1970s, but under different names. The concept of fugitive species is consistent with the tolerance succession model, where highly dispersive species that are poor competitors are the first to establish in recently disturbed sites (Elton 1927, Hutchinson 1951, Horn and Mac Arthur 1972). These early successional niches become unavailable to fugitive species as slower-dispersing, strong competitors arrive at the site and competitively exclude the fugitives. Southwood (1977) listed 11 synonyms of fugitive species, in addition to his focus on r life history strategies from MacArthur and Wilson's (1967) r-K spectrum. The new developments in succession theory (Connell and Slatyer 1977) were inhibited by the lack of cross-referencing to pre-existing terms for the same phenomenon.

Although we do not know the circumstances in which the tolerance model of succession was developed, there are two possible reasons to explain why new, redundant theory might be developed; (1) researchers genuinely may not recognise that a particular phenomenon is already well studied because the phenomenon has previously been described using a different theoretical framework and terminology; or (2) pre-exisiting terms and case studies may be ignored or overlooked to make the newly presented idea appear novel, with rewards in terms of publication in leading journals and high citation rates as the originators of new theory. Either way, research progress is slowed by redundant theory.

In the next three sections, we propose responses and solutions to the weak predictive success of theory, the planning and framing constraints, and the communication conundrums (Table 1). We summarize these solutions in a conceptual framework to illustrate how the solutions can be integrated with ongoing research (Fig. 1).

PREDICTION: SOLUTIONS

A primary motivation for developing and testing theory in any field is to make predictions about new cases (Peters 1991). To date in ecology, the ability to make accurate predictions has often proven to be an unrealistic expectation (e.g. Lindenmayer et al. 2003). Optimistically, we regard this as a lack of progress, rather than as affirmation of the general nature of ecological theory relative to the idiosyncrasy of ecological systems (Shrader-Frechette and McCoy 1993, Doak and Mills 1994). There are many case studies where particular theory **does** apply, and so progress requires understanding the scope of application of theory, and not in discovering a theory that has universal application across nature (Pickett et al. 1994).

The systematic review approach advocated by the Collaboration for Environmental Evidence (Pullin and Knight 2009), or collaborative reviews such as those undertaken by the National Center for Ecological Analysis and Synthesis in the USA (Reichmann 2004) could be readily adapted to fulfill the role of defining the bounds within which particular theories apply, including the temporal, geographic, environmental and taxonomic bounds. These review approaches may be strengthened in topic areas where there is currently substantial redundancy by resolving the communications flaws in the way theory is used. All case studies could then be flagged with agreed key words associated with rationalized theory, eliminating the risk that relevant studies could remain hidden by alternate sets of words associated with redundant theory. The aim of systematic or other reviews would be to describe contingent theory, such as in edge effects theory, where contingency may be related to the degree of habitat loss and fragmentation or the relative availability of resources across edges (Batary and Baldi 2004, Ries et al. 2004).

Lawton (1999) argued that developing predictive theory contingent on circumstances could be most successful in macro-ecology. Such contingent theory might be quite useful for macro-conservation such as continental or global reserve design. However, most conservation biology is focused on population, species and community level processes. The prospects for developing contingent theory may be reasonable for population processes, but dismal for the more complex interactions that are typical at a community level (Lawton 1999, Simberloff 2004). Developing contingent theory with predictive value remains a worthy goal (Shrader-Frechette and McCoy

1993). However, if common themes do not emerge through reviews of theory, the approach we have outlined will still remain valuable for demonstrating the absence of predictable contingencies, with the implication that data must be collected for each case study because best-guess management decisions based on theory do not exist.

The extent to which best-guess management decisions exist needs to be more effectively communicated to managers, policy makers and more broadly, to avoid the perverse outcomes that are possible when theory is applied inappropriately. Mechanisms for achieving improved science communication have been widely discussed. Cash et al. (2003) established a framework for improving knowledge transfer that included maximizing the salience, credibility and legitimacy of the messages provided by scientists. Communicating across the science-policy or science-management divide requires a range of boundary-spanning actions, such as cross-institution collaboration (Cash et al. 2003, van Kerkhoff 2005, Roux et al. 2006, Reyers et al. 2010), scenario-planning (Vanston et al. 1977, Peterson et al. 2003, Cumming 2007, Palomo et al. 2011), delivering information across the boundary in a salient format (McNie 2007, Likens 2010) and actions to develop personal relationships across institutions (Gibbons et al. 2008b). Broad public engagement (Salzman 1989, Pace et al. 2010) via a range of mechanisms (Groffman et al. 2010, Nisbet et al. 2010) is also an important aspect of boundary-spanning, particularly because public education contributes to shifting national norms (Reyers et al. 2010). Scientific organisations and government agencies both can play important roles in knowledge transfer (e.g. Calow et al. 1990, Vitousek et al. 1997, Osmond et al. 2010, Pouyat et al. 2010, Driscoll et al. 2011), but improved boundary-spanning often requires reforms to academic and government job performance indicators (Gibbons et al. 2008b, Cummings et al. 2010, Pace et al.

2010, Whitmer et al. 2010). Reducing the misapplication of theory therefore requires a sophisticated approach to boundary-spanning, in addition to the improved use and understanding of theory among ecologists.

RESEARCH PLANNING AND FRAMING: SOLUTIONS

Given the evidence that theory can be a heuristic "strait-jacket", a new approach is needed to break out of the "asylum" of specific theories. The planning and framing value of theory could be made redundant by adopting a list of phenomena or questions that researchers should consider when planning applied ecological research. For example, in considering the role of theory in restoration ecology, Palmer *et al.* (1997) reduced the heuristic value of two ecological theories into two salient questions. First, the "field of dreams" hypothesis predicts that providing a suitable physical environment enables species to colonize restored land, leading to the question: Are there critical thresholds of physical habitat restoration? Second, the initial floristics model of succession predicts that only species actually placed into a site at the beginning of restoration will remain over time, suggesting the question: At what spatial scale do we need to restore species diversity (Palmer et al. 1997)?

A broad, but simple and widely recognized checklist of concepts or questions would remove the emphasis from popular theories with their built-in assumptions about how systems function and direct attention to a full range of possible phenomena that should be considered in research and management planning. There are few examples that might qualify as such a list in the literature (e.g. Schoener 1986, Grimm and Wissel 1997, Schulte et al. 2006, Lindenmayer et al. 2008a). Guisan and Thuiller (2005) listed factors to consider in spatial distribution modeling including climatic limitations, dispersal, disturbance, resource availability and species interactions. Although different lists may be most pertinent in different contexts, it should be possible to develop generic lists applicable across a broad field of study.

As a step towards a generic list that could provide a heuristic framework for ecological research into species' conservation, we build on Guisan and Thuiller's (2005) list to suggest a broad set of guiding questions (Table 2). By considering this range of questions and, importantly, the many possible interactions, research planning in applied ecology can maintain a broad conceptual basis that avoids the heuristic limitations of individual theories. The eight questions that we have listed (Table 2) are not conceptually mutually exclusive. For example, population demographics determine abundance and survival and so are implicated in most of the other questions. However, we think this relatively short list draws attention to most of the key areas that are important for ecological research in species conservation, with minimal repetition and therefore may be adequately generic to provide planning support for a broad range of studies. More detailed lists of phenomena may be needed to 'unpack' our broad list, such as the many ways that predators and prey may interact depending on their degree of specialization and dispersal capacity (Taylor 1990, Ryall and Fahrig 2006). Further, our list may be nested within, or work in parallel with, checklists focused on community or ecosystem levels of organization, such as that developed by Grimm et al. (1997) for describing stability phenomena.

After a broad list of phenomena is developed, the second step in research planning is to make the list operational. A set of conceptual models is needed that reduce the array of possible phenomena into a framework of plausible phenomena relevant to the case study. The third step in research planning would then be to develop testable questions about pertinent aspects of the system based on a conceptual model of that system (Lindenmayer and Likens 2009). These new case studies would be interpreted using an inductive approach ("one must confront the facts of a particular situation, and then look for a way to make sense of them." p. 123, Shrader-Frechette and McCoy 1993). After an initial inductive approach reveals theories that are likely to apply, a hypothetico-deductive approach may then yield further insights into how the system works through secondary case studies (Fig. 1).

Encouraging ecologists to adopt this approach may require recognition by journal editors and reviewers that using a checklist for framing new research is a legitimate and often better approach than using conceptually narrow theory. Ecologists may also be encouraged by past case studies that have used an approach similar to the one we have described. For example, discovering acid-rain impacts in the Hubbard Brook Experimental Forest in New Hampshire, USA was based on research questions arising from a conceptual model of the system, not ecological theory (Likens and Bormann 1995, Lindenmayer and Likens 2009). Checklists are frequently presented in ecology-related papers, and sometimes are well received and highly cited (Grimm and Wissel 1997, de Groot et al. 2002, Lindenmayer et al. 2008a). Ecologists may therefore be amenable to taking the small additional step of using a checklist for planning and framing research.

COMMUNICATION AMONG SCIENTISTS: SOLUTIONS

In the short term, journal editors and reviewers could help to reduce the growth of redundant theory by demanding that authors fully justify any new terms or theory in the context of all preceding theories that address related phenomena. However, a new series of syntheses is needed to help rationalize the existing surplus of overlapping and redundant theory and to define terms. In cases where multiple theories explain the same process leading to isolated enclaves of research, work is needed to draw together those currently separate fields by building a unifying set of concepts and eliminating redundant terminology. Importantly, such rationalization of theory needs to focus on ecological phenomena (e.g. disturbance) rather than a defined area of theory (e.g. the intermediate disturbance hypothesis). Reviews need to gather together all of the theories that describe a particular process or pattern and then build a synthesis of the collected overlapping, complementary and redundant theories. The aim of these syntheses would be to define the minimum theory set that describes particular phenomena and to position the rationalized theory within the broader framework of other syntheses, demonstrating any links and nested relationships. This approach is similar to the method of 'integration' across ecological fields advocated by Pickett et al. (1994), but places emphasis on consolidating existing understanding into more efficient frameworks. This approach also has analogues in the data-mining literature, where discoveries can be more efficient if a set of non-redundant search rules are used (Lo et al. 2009), and in nursing where theoretical concept analysis (Risjord 2009) is used for clarifying the definitions and use of terms in support of theory development. The benefits of rationalization of ecological theory are that theory would be more accessible, it would provide a coherent basis for choosing particular theory, and would break down the conceptual and communications barriers between fields that address the same phenomena.

Components in the rationalization of theory might include (1) a scope defined by a phenomenon or interactions among them; (2) a collation of theories and terms used to describe the phenomenon, and; (3) synthesis. The synthesis would remove redundancy, formulate competing explanations into a single framework, link that framework to pre-existing rationalizations of theory and provide definitions. As a simplified example, (1) the scope could be defined as a pattern of complete occupancy of all of the available niche or 'preferred' habitat. (2) Some relevant theories describing this pattern include niche theory, the metacommunity species-sorting concept, and the storage effect (Warner and Chesson 1985). (3) A synthesis would identify and remove redundancy in niche theory and the metacommunity species-sorting concept (both imply a high level of dispersal and good establishment). The synthesis would also build a framework that links to broader rationalizations of theory (if they existed) and would recognize that the storage effect and niche theories are competing mechanisms. This third component therefore guides the synthesis to distinguish between theories that use different words to describe the same phenomenon (and are therefore redundant, e.g. mass effects versus spill-over edge effects) and theories that present different mechanisms to describe the same process or pattern (and are therefore competing, but not redundant).

This approach to rationalization of theory probably will not, by itself, resolve the expansion of redundant theories and associated terms. If novelty remains a pre-eminent criterion for publishing success, then authors will be motivated to label established phenomena with new theory based on hair-splitting or inadequate knowledge of previous work (Belovsky et al. 2004). Further, Hodges (2008) argued that the main reason past attempts to rationalize the use of ecological terms have failed is that subsequently, ecologists have not accessed the most up to date definitions. This problem could be minimized if syntheses were managed using agreed protocols and were made widely available through a centralized reputable organization (Fazey et al. 2004).

A centralized organization for theory synthesis could be modeled on a number of existing collaborations. For example, in the medical field, the Cochrane Collaboration provides a central, widely used and respected repository for systematic reviews of medical interventions (Bero and Rennie 1995). More recently, the Collaboration for Environmental Evidence has established this model for conservation and management interventions (Pullin and Knight 2009), and is rapidly growing in scope and impact (CEE 2010). In forestry, an authoritative dictionary of 4500 words is maintained through international collaboration by the Society of American Foresters (Helms 1998). Each of these collaborations involves leading researchers in the field, ensuring quality and legitimacy, and provides a central web-based location where reviews or definitions can be readily retrieved.

The International Nucleotide Sequence Database Collaboration (http://www.insdc.org/) presents another model of international scientific cooperation that a new collaboration for ecological theory might learn from. The INSDC involves cooperation of three organizations that catalogue and make available genetic sequence data submitted by researchers from around the globe (Cochrane et al. 2011). Important elements that could be adapted in an ecological theory collaboration are the free sharing of information, voluntary international cooperation, the use of multiple hubs to ensure wide participation and data security, knowledge collation based on peer-reviewed publications, and a strong link between acceptance by journals and author participation in the collaboration (through the INSDC accession number system, Cochrane et al. 2011).

An authoritative and accessible structure inspired by existing models such as CEE, and INSDC, would expedite the rationalization of ecological theory. Major national and international ecological organizations may have the capacity and authority to develop a collaboration that would be widely respected by ecologists (e.g. Ecological Society of America, International Association for Ecology, the Society for Conservation Biology, other major national ecological societies). Such a collaboration would enable existing theory to be elaborated, refined, or overthrown when necessary, and ensure that only truly new ideas made it into the revised rationalization. It could provide a forum for debating and updating definitions of ecological terms. Importantly, with a single repository for theory, all ecologists would know where to access the most up-to-date ecological theory and definitions, and would have a framework for selecting an appropriate theory that describes their case study. A central repository for theory and definitions would also be a valuable new source of credible and salient information (Prendergast et al. 1999, Cash et al. 2003, Janse 2008) for application in spanning the boundaries between science and management.

PERSPECTIVES FROM LONG TERM RESEARCH

The following section comprises two case studies that illustrate many of the problems and some of the solutions in prediction, planning and communication that we have discussed. The case studies are unusual in that a wide range of ecological theories have been tested using extensive and often long-term empirical data (summarized in Lindenmayer 2009a, b). These long-term studies provide a rare opportunity to examine how theory has been used in making predictions, in developing research, and in communicating theory.

Case study #1 – The Tumut Fragmentation Study

The Tumut Fragmentation Study in southern New South Wales, south-eastern Australia, commenced in 1994 and continues today. The study has focused on the occurrence and dynamics of mammals, birds, reptiles and other taxonomic groups within a landscape dominated by plantations of exotic *Pinus radiata* (Lindenmayer 2009a). The study at Tumut includes 86 remnant patches of *Eucalyptus* forest stratified by patch size, shape, forest type, and time since fragmentation. In addition, the study includes 40 “control” sites located within large areas of unfragmented eucalypt forest and 40 sites in the plantation “matrix” surrounding the patches of remnant eucalypt forest (Lindenmayer 2009a).

Prediction — There are several examples of species from the Tumut study that support metapopulation predictions such as by showing expected relationships with patch size and isolation, including fitting incidence-function models (Lindenmayer et al. 1999c, Lindenmayer et al. 2001). However, many species were not primarily influenced by landscape features of a patch-matrix model. The occurrence of some bird and marsupial species was poorly predicted by metapopulation models because they occurred throughout the matrix or were very widely dispersing (Lindenmayer et al. 1999c, Lindenmayer et al. 2001). Patch size and isolation was unimportant for frog species, which were instead strongly influenced by the location of wide, shallow swamps (Parris and Lindenmayer 2004). Further, Fischer et al (2005) showed that a habitat continuum model including food, shelter, space and climate axes described the abundance and distribution of reptiles in the Tumut study better than the patch-matrix model.

A range of theory in addition to metapopulation theory has been tested using the Tumut study system (Table 3). In general, ecological theory has been poorly supported, and when theory was consistent with field evidence, it was usually for only a subset of species and circumstances. One exception was the peninsula effect (Simpson 1964), which involved a simple test of changes in species richness of one taxon (birds). Our experience in challenging ecological theory with field data from Tumut strongly reinforces our argument that ecological theory often has limited predictive value.

With limited predictive ability, application of popular theories to management in the Tumut study led to poor management decisions initially, but with sustained boundary-work (sensu Guston 1999), better outcomes have been achieved. At the outset of the project, managers came into the planning room with the idea that there is a minimum patch size warranting protection. This pre-conception arose from an understanding of island biogeography and nested subset theory, both of which predict that small patches will have fewer species and, under nested subset theory, species in small patches are a subset of those in larger patches (Cole 1983). This meant that small patches could be cleared to reduce impediments to pine plantation establishment with no impact on conservation values (this argument had also been made in North America based on island biogeography theory, see Simberloff 1988). Subsequent research demonstrated that nesting of the biota was weak in the Tumut study system, and small remnants had conservation value that larger remnants did not (Fischer and Lindenmayer 2005). This new message about the importance of small patches was communicated to managers on field days, and to corporate planners during meetings in city office towers. As a consequence, the minimum size of patches that must be retained during plantation establishment was reduced from 10 ha to 1 ha. This is a critical change because plantation expansion in the Tumut region targets former grazing land that supports many small patches of threatened woodland communities (Lindenmayer et al. 2008c).

Research Planning and Framing — The work at Tumut commenced as an investigation of landscape context and habitat fragmentation, a choice that was strongly influenced by metapopulation theory (Lindenmayer et al. 1999b). This initial focus and extensive research effort based on a patch-matrix model (e.g. Lindenmayer et al. 1999c, Lindenmayer et al. 2001) may have slowed progress towards improved plantation management. Fragmentation concepts make the assumption that the matrix is inhospitable, without beneficial effects for patch-based species. However, the strong influence of the matrix on population survival in patches was revealed in a matrix harvesting experiment (Lindenmayer et al. 2009). Birds and one marsupial declined in patches when the entire surrounding pine matrix was harvested, but not if only half of the surrounding matrix was cleared. Through negotiation with land managers, these findings have recently led to the spatial re-scheduling of harvesting around patches. We speculate that these insights may have been gained more quickly (and embraced more quickly and earlier by plantation managers) if a checklist of research planning questions had been followed. A checklist would have encouraged an early focus on the possible role of the pines as habitat, rather than the focus on patch-matrix-based theory. Nevertheless, we acknowledge that the delay in progress was short, because results that contradicted patch-matrix assumptions quickly accumulated. The "metapopulation approach" to research in fragmented landscapes (Hanski and Gaggiotti 2004, Driscoll 2007) is probably the most sophisticated approach to landscape scale research that is based on ecological theory. In some situations, the metapopulation approach may be as good (or almost as good, in the case of Tumut) as a checklist approach because the approach emphasises a broad range of questions.

Communication Among Scientists — There is some evidence supporting limited communication among theoretical fields arising from the Tumut research. A major publication examining bird distributions at Tumut was framed in the context of "fragmentation" (Lindenmayer et al. 2002b). However, this study had important implications for metacommunity theory, where mass effects strongly influenced the bird community in pines adjacent to eucalypt remnants and where species-sorting and potentially patch-dynamic processes drove some species to be most abundant in the smallest patches, or in intermediate-sized patches. Further, there was no evidence of any spatial dependence, originally interpreted as evidence against a mainland-island metapopulation, but also important evidence that neutral metacommunity processes are not predominant. Despite these important implications for metacommunity theory, only four of 97 papers that cited Lindenmayer et al (2002) have a metacommunity focus (and three of these were written by us). In contrast, aligned with the fragmentation framing of the paper, 71 of the citing papers include fragmentation as a searchable term. As a second contrast, a paper with metacommunity in the title and published in the same year (Mouquet and Loreau 2002) was cited 143 times, with 67 of the citing papers including "metacommunity" in the abstract, keywords or title. We speculate that if Lindenmayer et al. (2002) had placed emphasis on metacommunity theory in the abstract and discussion, that these important insights into metacommunity processes would have been more regularly cited in the growing metacommunity literature.

Case Study #2 – Wet Forest in the Victorian Central Highlands

Our second case study focuses on the wet forests of Victoria, south-eastern Australia, where research commenced in the early 1980s (reviewed by Lindenmayer 2009a). The core of the study consists of 161 sites that have been surveyed on a repeated basis over the past 27 years for arboreal marsupials and vegetation structure (Lindenmayer et al. in press) and ten years for forest birds (Lindenmayer 2009b). Most sites are dominated by Mountain Ash *Eucalyptus regnans* or Alpine Ash *E. delegatensis*, with a wet sclerophyll forest or cool temperate rainforest understory (Ashton 2000). An array of projects has been completed and others are ongoing. These include studies of old growth forest (Lindenmayer et al. 2000), the rate of collapse of large trees with hollows (Lindenmayer et al. 1997, Gibbons et al. 2008a), the use of large trees with hollows by arboreal marsupials (Lindenmayer et al. 1990b, Banks et al. 2011c), post-fire ecological recovery (Banks et al. 2011a, Banks et al. 2011b) and the influence of variable retention harvesting on small mammal populations (Lindenmayer et al. 2010).

Prediction — The development and use of theory in the wet forest research provides a case in point similar to that proposed in Figure 1. In Figure 1 we suggest that initial research should be developed in an atheoretical context using a checklist, and then theories relevant to the initial data sets can be identified and further tested (steps 4-5 in Fig. 1). Much of the wet forest research has made little or no use of theory. Instead, the research is framed around specific problems about habitat use and resource provision. However, emerging from this approach are two areas of theory that have successfully aided interpretation, reframing and further testing of predictions. First, the influence of phenomena at a hierarchy of spatial scales was evident from over a decade of research into Leadbeater's possum *Gymnobelideus leadbeateri*, a threatened species

(Lindenmayer 2000). This 'hierarchy theory' (Allen and Starr 1988) was effectively applied to model the possum's spatial distribution (Mackey and Lindenmayer 2001) and forms an important component of subsequent checklists for guiding forestry research (Lindenmayer et al. 2006). Second, the reliance of arboreal marsupials on tree hollows (Lindenmayer et al. 1990b) in an ecosystem strongly affected by fire and post-disturbance logging revealed that large trees remaining after disturbance provide critical resources for Leadbeater's possum. These observations contributed to the emergence of 'biological legacy theory', which predicts that the outcome of disturbance is mediated by the resources that linger afterwards (Franklin et al. 2000, Franklin et al. 2002, Lindenmayer and Ough 2006). In the Victorian wet forest, like at Tumut, reasonable predictions could not be made using "off the shelf" theory (Table 4). However, theory that arose from detailed empirical work in the wet forest study system could be applied to make predictions about that system and to reframe ongoing research.

Predictions from theory have not generally featured in the management of the wet forest study system. Nevertheless, a number of important lessons about effectively engaging with managers have been learned. Particularly, one form of science communication has not worked – providing reprints of scientific articles to resource managers and conservation practitioners. These are not read by either group. Our experience is consistent with other research in which resource managers based their management decisions on experience and not on written scientific outputs (Sutherland et al. 2004, Fazey et al. 2006), a situation that has a broad range of underlying causes (Jasanoff 1987, Cash et al. 2003). In contrast, perhaps the most effective science-communications strategy has been to use grant funding to permanently base a research officer in the field. The person serves a boundary-spanning function by working full-time on the research program but staying connected on a daily basis with resource managers from government agencies (boundary-work, Guston 1999). With high turnover of staff in agencies, this capacity for regular communication has proven invaluable for briefing new staff about ongoing research. Effective communication is also facilitated by regular field workshops, enabling a two-way dialogue with agency personnel. Some workshops have become major international meetings and provided a setting in which new forest management initiatives have emerged (Lindenmayer et al. 2004). In addition to organizational boundary-spanning, public outreach has been a feature of both the wet forest and Tumut research programs (e.g. Lindenmayer and Possingham 1995b, Lindenmayer et al. 2008b). We have found that books, plus posters and brochures, are more salient boundary-spanning objects for research users and managers than peer-reviewed scientific articles (Cash et al. 2003, McNie 2007).

Research Planning and Framing — The wet forest research commenced as an applied investigation into the habitat requirements of Leadbeater's possum (Lindenmayer et al. 1990a). Early results showed that high quality possum habitat could be generated by retaining an adequate number of old trees in logging coupes (Lindenmayer et al. 1991). However, a strong focus on metapopulation modelling during the early and mid 1990s distracted from these initial coupe-level conservation recommendations. Metapopulation simulations emphasised the pre-eminence of whole patches for the survival of Leadbeater's possum (Lindenmayer and Possingham 1995a), resulting in conservation planning that focused on reservation. However, later evidence revealed that disturbed forest was more important for possum survival than previously assumed (Lindenmayer and McCarthy 2006). Building on the initial site-level phase and the subsequent metapopulation phase, a new imperative surfaced that emphasised features at three spatial scales: habitat features at the coupe-level, riverine buffers and corridors at the forest block level, and reserves at the regional level (Lindenmayer and Franklin 1997). This recognition meant that the initial emphasis on coupe-level management had to be revisited. New discussions between researchers and managers led to establishment of a variable-retention harvesting research project aimed at better integration of conservation with production at a fine spatial scale (Lindenmayer et al. 2004).

Rather than having to go through this learning process with the associated delay in introducing the variable-retention harvesting idea to Victorian forest managers, we believe in hindsight that faster progress might have been expected if a checklist of research questions had been used from the outset. With a checklist (e.g. Lindenmayer et al. 2006), all scales would have been examined earlier on, ensuring that the emphasis on coupe-level structure was maintained throughout the research program. It could be argued that a useful checklist of questions may not have emerged first without a detailed series of tests of different areas of ecological theory. Regardless of the truth of such an argument, there is no need for future research to suffer the same delays and opportunity costs associated with sequential testing of sometimes overlapping, sometimes disconnected ecological theory.

Communication Among Scientists — There is evidence from the wet forest study that linking observations to appropriate theory enhances communication of the observed phenomenon. Lindenmayer and Possingham (1996) present an early and clear description of the biological legacy concept without using the term "legacy". The term "biological legacies" first appears in the same context in which we use it (Franklin et al. 2002) in Lee et al. (1997) . Lindenmayer and

Possingham's (1996) metapopulation model identified the importance of dead trees for reducing extinction risk of Leadbeater's possum after fire. However, that study has not been cited by papers that also used "biological legacies" as a searchable term. This contrasts with other papers that draw on the wet forest case study and specifically mention biological legacies (Franklin et al. 2002, Lindenmayer and McCarthy 2002, Lindenmayer and Noss 2006, Lindenmayer and Ough 2006), for which 9-14% of citing papers also mention biological legacies. If one wished to review phenomena associated with the biological legacy concept, the latter papers would be readily discovered, but the earlier modelling work may not be.

Case Studies – summing up

The Tumut and Victorian wet forest case studies provide support for our key concerns about the application of theory in conservation, namely: theory has little predictive value when applied in new situations, theory can constrain research progress when used to plan research, and theory can limit communication when multiple sets of terms are used to describe the same phenomenon. However, the case studies also provide important insight into how theory can be used effectively in the research cycle, particularly for prediction after an initial phase of research has identified relevant theory, and for communicating important concepts with ecologists and with managers, reducing the risk that theory will be applied perversely.

CONCLUSIONS

To make faster progress in applied ecology, three important steps are to: (1) better define the predictive capacity of theory, and therefore better identify appropriate applications by: publishing reviews that define contingent theory, refine rationalized theory and provide support for decision-making; (2) guiding research planning and framing by: encouraging applied ecologists to use a broad checklist approach when planning new research and to use rationalized theory more widely in new and secondary case studies, and; (3) enhance communication among scientists by: developing and updating rationalized theory from which redundant theory has been purged, and for which a set of key-word definitions are developed.

Implementing these steps effectively will likely require careful management through international collaboration. A collaboration for ecological theory could draw on many of the principles and mechanisms of existing international science partnerships, including those of the Centre for Environmental Evidence and the International Nucleotide Sequence Database Collaboration. A co-operative institution built around a number of existing respected scientific organizations could make rationalized theory, definitions and checklists for research planning widely available, which is an essential component of limiting redundancy, improving communication, and providing a tool to support boundary-spanning actions.

By implementing these three steps, research progress will be accelerated through increased capacity to discover contingent theory, through routine use of a broad conceptual scope in research planning and framing, and by access to improved tools for communication among ecologists. With these improvements in prediction, research framing and communication, ecologists will have better tools for application in spanning the boundaries between ecologists, managers and policy makers.

Many of the approaches that we have advocated are likely to be beneficial in fields outside of applied ecology. Redundant theory and terminology is likely problematic across all disciplines (e.g. occupational health: Gronqvist et al. 2001, social sciences: Bentrupperbaumer 2006, medicine: Makoul and Clayman 2006, nursing: Mantzoukas and Watkinson 2007, engineering: White 2007, psychology: Cherniss 2010, geology: Ramsey 2010). Most fields are therefore likely to benefit from establishing both collaborative centralized coordination and dissemination of rationalized theory and terminology.

Removing the impediments to research progress that are embedded in the way applied ecologists currently use theory is now very important because these limitations abet inappropriate application of theory in conservation. We think that the framework we have presented would help to avoid management mistakes and increase the capacity of ecologists to rise to the challenges of biodiversity conservation in the face of global change.

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Table 1. Three important ways that theory should contribute to conservation biology, the reasons it often fails to make that contribution, and the changes that would help to resolve those problems.

How theory should help	**Why theory often fails**	**Solutions**
Predict outcomes of new situations	There are no universal laws and there is a poor understanding of contingencies	Systematic review to clarify application of theory and develop contingent theory
	Theory is applied regardless of these failings, with a risk of perverse outcomes	Improved science-practitioner boundary spanning, combined with other listed solutions
Heuristic value: provide understanding for planning research and posing research questions	Theory has narrow conceptual scope, constraining thought and planning	Avoid use of theory for guiding initial or broad research programs by using a list of phenomena or questions instead (Table 2)
Communicate findings across taxa, regions and biomes using a common set of terms and concepts	Redundant theory isolates researchers and undermines a logical choice of framework	Rationalization of theory through synthetic review of the theory describing a set of phenomena
	Poorly defined terms confuse discussion	Develop authoritative dictionary of key words

Table 2. The heuristic value of many theories used in conservation could be replaced by three classes of questions; regional and landscape phenomena, abiotic drivers and biotic processes. These provide a broad conceptual basis for research development in species management and conservation, ensuring that a broader range of phenomena are considered than when research is developed within the domain of a particular theory. From this checklist of questions about phenomena, researchers can develop a conceptual model of their system and use that conceptual model to formulate focused and relevant research questions (Lindenmayer and Likens 2009).

Phenomena at Regional and Landscape Scales

Regional fluxes. What regional processes influence the species within the focal landscape? (Region defined as the area surrounding a focal landscape and landscape defined from a management or species perspective. e.g. influx of resources and species from outside the focal landscape.)

Landscape elements. Which parts of a landscape are used by the species and for what purpose? Are there gradients or patch-matrix patterns of occupancy and are landscape elements used as sources, sinks, or for dispersal or foraging? These questions aim to define aspects of a species' habitat and describe its location in the landscape.

Abiotic Drivers

Environment. Do species respond to environmental gradients or variation across the landscape? (e.g. temperature, rainfall, nutrients)

Disturbance. How do disturbance regimes influence species abundance and survival? (type of disturbance, frequency, extent, severity, duration (Shea et al. 2004), e.g. climate change, drought, flood, fire, wind, anthropogenic impacts)

Time. What is the appropriate temporal scale for examining ecological responses? (Considerations include the rates and relative impact on population survival of all other processes)

Biotic Processes

Interactions. To what extent do interactions with other species influence abundance or survival? (prey, predators, competitors, pollinators, seed dispersers, pathogens, hosts, vegetation structure)

Dispersal. How does dispersal influence abundance and survival of populations? (immigration, emigration, colonization)

Demographics. What are the characteristics and main drivers of population demographics? (characteristics: population growth, recruitment, survival, population extinction; main drivers: interactions with abiotic and other biotic processes, genetic effects, life history)

Table 3. Ecological theory that has been tested using the Tumut study system

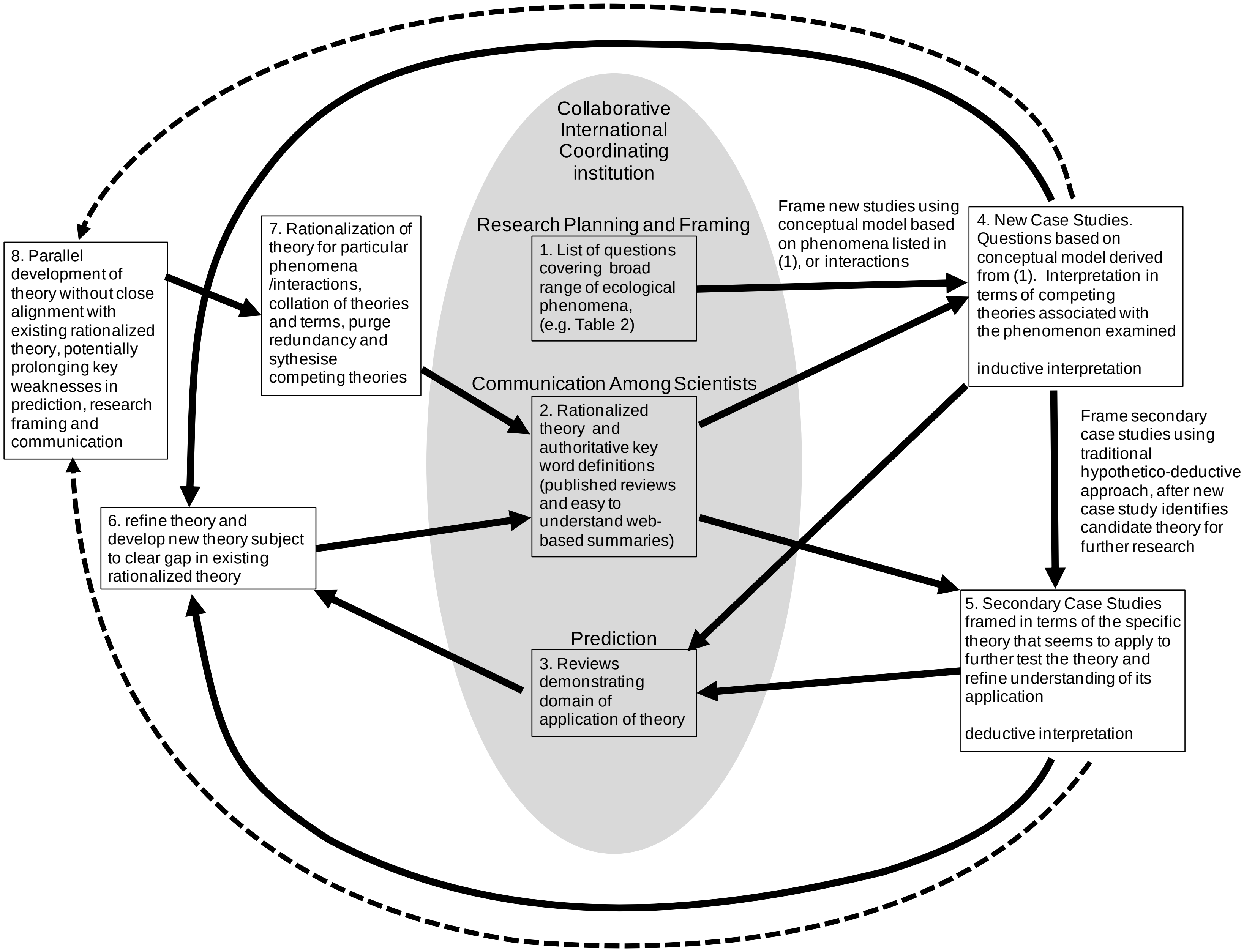
Theory	Test methods	General findings	Reference
Metapopulation	Tested fit of PVA and incidence function models	Occurrence of some birds and mammals well predicted, others poorly predicted. No general patterns in which kinds of species conform to theoretical assumptions.	(Lindenmayer et al. 2003)
Ecological Thresholds	Incidence under different proportions of vegetation cover	No species exhibited the predicted threshold response because the assumption that vegetation = habitat was not correct.	(Lindenmayer et al. 2005)
Nested Subset	Nestedness in birds, reptiles and possums	Possums and reptiles were not nested, and birds were imperfectly nested due to occurrence in the matrix, and effects of temperature gradients for reptiles.	(Fischer and Lindenmayer 2005)

Metacommunity	Rare species and community changes across an isolation gradient	Competing metacommunity concepts act ephemerally, sometimes simultaneously, and effects vary with species and region.	(Driscoll and Lindenmayer 2009)
Peninsula effect (derived from island biogeography)	Measure abundance along narrow eucalypt remnants	Only tested with birds, and found decreasing species richness with distance along peninsulas as predicted by theory	(Tubelis et al. 2007)
Ecological resilience	Compared resilience statistics in landscapes with different land-use intensification	Predictions that Tumut fragments should show lower resilience measures for bird communities than Tumut controls were not observed.	(Fischer et al. 2007)
Assembly Rules	Tested for positive and negative relationships among bird species after taking into account vegetation differences	Almost no evidence of negative interactions at Tumut, and effects ephemeral. Assembly rules had no predictive value.	(Driscoll and Lindenmayer 2010)

Table 4. Ecological theory that has been tested using the Victorian wet forest study system

Theory	Test methods	General findings	Reference
Surrogates and Indicators	Indices of proximity to settlement, intensity of land use, other arboreal marsupials as biodiversity surrogates	No relationship between surrogate and occurrence of possum species	(Lindenmayer and Cunningham 1997, Lindenmayer et al. 2002a)
Ecological resilience	Compared resilience statistics in landscapes with different land-use intensification	Incorrectly predicted higher resilience than a randomly assembled community in the wet forest system	(Fischer et al. 2007)
Assembly Rules	Tested for positive and negative relationships among bird species after taking into account vegetation differences	No negative interactions between bird species were observed in wet forests. Assembly rules had no predictive value.	(Driscoll and Lindenmayer 2010)
Metapopulation	Applied in a series of studies, not explicitly tested.	New empirical research showed that patch-matrix assumptions applied to one possum species, but not three others, or most bird species.	(Lindenmayer and Lacy 1995, Lindenmayer and Possingham 1995a, Lindenmayer et al. 1999a, McCarthy and Lindenmayer 1999, Lindenmayer 2009b)

Figure 1. Conceptual model of how solutions to the three key areas in which theory often fails can be incorporated into research. An international coordinating institution (grey oval) provides an authoritative central repository and access point for three classes of information: (1) a list of questions describing phenomena that are important to consider in developing and framing research (e.g. our Table 2), (2) peer-reviewed rationalized theory and definitions of key words that facilitate better communication among scientists, and (3) systematic reviews that develop contingent theory with the potential for prediction. New case studies (4) use a conceptual framework based on the list of questions (2) for framing and planning to avoid using particular theories with narrow heuristic scope. New case studies are interpreted and relevant theories identified using an inductive approach, then theories are further tested in secondary case studies (5) using a hypothetico-deductive approach. New case studies, secondary case studies and systematic reviews of theory may provide new insight that refines theory or requires development of new theory (6). Rationalized theory may thereby be updated, possibly through a peer-review process within the coordinating institution, ensuring that the most comprehensive theoretical frameworks are readily accessible. The systematic rationalization of theory (7) plays the dual role of setting up the frameworks for using theory throughout the research cycle, and of enabling periodic review of the theory describing particular phenomena in addition to the gradual refinement that might arise through (6). If new research does not refer to rationalized theory, or in fields where rationalized theory has not been published, the ongoing parallel development of theory is likely (dashed lines, 8), providing new motivation and source material for additional syntheses to rationalize theory (7).


Collaborative International Coordinating institution
Research Planning and Framing
1. List of questions covering broad range of ecological phenomena, (e.g. Table 2)
Communication Among Scientists
2. Rationalized theory and authoritative key word definitions (published reviews and easy to understand web-based summaries)
Prediction
3. Reviews demonstrating domain of application of theory
Frame new studies using conceptual model based on phenomena listed in (1), or interactions
4. New Case Studies. Questions based on conceptual model derived from (1). Interpretation in terms of competing theories associated with the phenomenon examined
inductive interpretation
Frame secondary case studies using traditional hypothetico-deductive approach, after new case study identifies candidate theory for further research
5. Secondary Case Studies framed in terms of the specific theory that seems to apply to further test the theory and refine understanding of its application
deductive interpretation
6. refine theory and develop new theory subject to clear gap in existing rationalized theory
7. Rationalization of theory for particular phenomena /interactions, collation of theories and terms, purge redundancy and sythesise competing theories
8. Parallel development of theory without close alignment with existing rationalized theory, potentially prolonging key weaknesses in prediction, research framing and communication