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Resilience of New Zealand indigenous forest fragments to impacts of livestock and pest mammals

Mike Dodd^{1*}, Gary Barker², Bruce Burns³, Raphael Didham^{4,5}, John Innes², Carolyn King⁶, Mark Smale² and Corinne Watts²

¹AgResearch Grasslands, Private Bag 11008, Palmerston North 4442, New Zealand

²Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand

³School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

⁴School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

⁵Present Address: School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia and CSIRO Entomology, Centre for Environment and Life Sciences, Underwood Avenue, Floreat WA 6014, Australia

⁶School of Biological Sciences, University of Waikato, Private Bag 3105, Hamilton 3240, New Zealand

*Author for correspondence (Email: mike.dodd@agresearch.co.nz)

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Abstract: A number of factors have combined to diminish ecosystem integrity in New Zealand indigenous lowland forest fragments surrounded by intensively grazed pasture. Livestock grazing, mammalian pests, adventive weeds and altered nutrient input regimes are important drivers compounding the changes in fragment structure and function due to historical deforestation and fragmentation. We used qualitative systems modelling and empirical data from *Beilschmiedia tawa* dominated lowland forest fragments in the Waikato Region to explore the relevance of two common resilience paradigms – engineering resilience and ecological resilience – for addressing the conservation management of forest fragments into the future. Grazing by livestock and foraging/predation by introduced mammalian pests both have direct detrimental impacts on key structural and functional attributes of forest fragments. Release from these perturbations through fencing and pest control leads to partial or full recovery of some key indicators (i.e. increased indigenous plant regeneration and cover, increased invertebrate populations and litter mass, decreased soil fertility and increased nesting success) relative to levels seen in larger forest systems over a range of timescales. These changes indicate that forest fragments do show resilience consistent with adopting an engineering resilience paradigm for conservation management, in the landscape context studied. The relevance of the ecological resilience paradigm in these ecosystems is obscured by limited data. We characterise forest fragment dynamics in terms of changes in indigenous species occupancy and functional dominance, and present a conceptual model for the management of forest fragment ecosystems.

Keywords: biodiversity; model; perturbation; system dynamics

Introduction

Lowland native forest fragments are the poorly represented remnants of one of the most damaged and threatened indigenous ecosystems in New Zealand (Craig et al. 2000; Ewers et al. 2006). Extensive destruction of the original forests during two human colonisation events has left a relictual landscape (*sensu* McIntyre & Hobbs 1999) in which these vegetation components are subject to repeated, severe perturbation events with no comparable historical analogue. Aside from the habitat loss and fragmentation process itself, these perturbations have included selective harvesting of certain canopy dominant trees (Nicholls 1979), intermittent browsing and soil disturbance by domestic livestock (Jane 1983), the introduction of pest mammals and plants (Craig et al. 2000), elevated rates of inorganic nutrient input via agricultural fertiliser drift and/or animal transfer (Stevenson 2004), altered hydrological regimes through drainage of the surrounding pastoral land (Whaley et al. 1997) and exposure to agricultural herbicides. With the exception of the initial logging, all of these perturbations can be regarded as ‘press disturbances’ (Bengtsson 2002), since the agents (in the case of livestock, pests, drainage, agrichemical and fertiliser transfer) or latent effects (in the

case of fragmentation) continue to operate for at least several decades and up to a century in some regions.

As a result of the combined effects of multiple perturbations, the structure and functioning of native forest fragment ecosystems have been highly modified. Canopy and subcanopy vegetation cover has been reduced and regeneration of canopy trees has been inhibited (Smale et al. 2005, 2008; Burns et al. in press), forest soil litter and organic layers have been reduced or removed, nesting success of all native bird species has declined or been prevented altogether (Innes et al. 2004; Boulton et al. 2008) and adult occurrence reduced to sporadic visits (Stevens 2006), indigenous plant species diversity has been reduced (Smale et al. 2008) and some plant and bird species have been extirpated (Whaley et al. 1997; Miskelly et al. 2008; Innes et al. 2010a). While the invertebrate fauna has been shown to remain relatively abundant and diverse in fragments dominated by indigenous plants (Crisp et al. 1998; Harris & Burns 2000), substantial dissimilarity in the composition of invertebrate taxa has been shown relative to more intact reference forests (Didham et al. 2009), with largely unknown effects on ecosystem functioning. It seems clear that without some countervailing intervention, native forest fragments will remain in a degraded state and

may eventually disappear from the lowland landscape, as the ageing population of indigenous canopy trees gradually dies out and the historical 'extinction debt' (Tilman et al. 1994) catches up with forest fragments surviving for the present under the prevailing landscape regime.

In this paper, we discuss whether this grim outlook for forest fragments is avoidable, given the small size of most fragments, the high degree of degradation that they have already sustained and the overwhelmingly adverse surrounding matrix environment in which they exist. Specifically, we question whether forest fragments can be restored to a self-sustaining structure and function that is characteristically indigenous, through management that releases them from the multiple perturbations they face. This is essentially a question about resilience (see Box 1), which is a key ecological concept relevant to understanding the nature and effects of ecosystem recovery following perturbations. We sought to determine whether there is good evidence that native forest fragments

exhibit the characteristics indicative of either of the types of resilience – engineering or ecological – described in Box 1. We did not seek to support or refute the validity of the concepts but rather to explore their relevance to the system of interest (Suding & Hobbs 2009). In order to develop sound management approaches for forest fragments, it is useful to understand how the inherent resilience of these ecosystems may be utilised, or may represent an obstacle to success, in achieving management goals.

More specifically, our objectives were to (1) explore the relevance of the two resilience concepts (Box 1) to indigenous lowland forest fragments; (2) assess the resilience of these forest fragments to the major perturbations resulting from stock and pest mammals; and (3) develop a conceptual management framework that might account for and utilise this resilience, in order to develop long-term strategies for conservation management of forest fragments.

BOX 1

Resilience concepts in ecology

Two concepts of resilience are most commonly seen in the ecological literature – engineering resilience and ecological resilience (Gunderson 2000; Bengtsson 2002). The first incorporates the ability of a system to recover its initial structure or character following a perturbation (Pimm 1984) and has been referred to as 'engineering resilience' because of its similarity to attributes measured in that discipline (Holling 1996). This more conventional concept of resilience assumes there is a global stability domain for a system property (i.e. the typical or 'normal' range in that system property observed over time or space as a result of environmental variation) that the system returns to naturally following a significant perturbation (see Fig. 1). Following a perturbation that leads to a deviation from this range, engineering resilience can be measured as the time taken for the property to return to the normal range (see Ludwig et al. 1996).

However, some ecosystems have been observed not to return to an expected global stability domain after perturbation, but have remained within an alternative stable domain, having crossed a hysteresis-type threshold (Suding & Hobbs 2009; Fig. 1). These observations led to the development of another resilience concept called 'ecological resilience' (Holling 1996). This concept of resilience sets aside the assumption of a single global equilibrium, in favour of multiple local equilibria (or domains of attraction). The commonly depicted visual model for the concept is a ball in a landscape of troughs and ridges, with the ball representing the system and the troughs representing alternative domains of attraction. Movement of the ball between troughs is described as a 'regime shift', since the controls on structure and functions have changed (Gunderson 2000). The most well-developed cases in ecology relate to rangeland grazing systems (with the background being the development of 'state and transition' models; Westoby et al. 1989) and lake systems (Walker et al. 1997; Scheffer & Carpenter 2003) but many others have been suggested (see Walker & Meyers 2004). Suding and Hobbs (2009) provide a useful summary and glossary of these concepts in the context of restoration ecology.

In the case of a regime shift the notion of a return time becomes meaningless, and the relative resilience of systems cannot be quantitatively assessed using this measure. It has

been suggested that a more appropriate measure of resilience in this context is the magnitude of the perturbation required to force the regime shift (Holling 1996). Any measure of resilience relevant to this scenario must consider the degree of deviation from the normal domain and how this changes over time. Orwin and Wardle (2004) have thoughtfully examined such measures and developed a mathematically and conceptually robust index.

For whichever concept of resilience one is working with, it is clear that resilience is a relative concept – there is only value in considering the relative resilience of either a specific ecosystem to multiple disturbances, or multiple ecosystems to the same disturbance. Hence there is a need to be specific about the system(s) and perturbation(s) of interest (Carpenter et al. 2001).

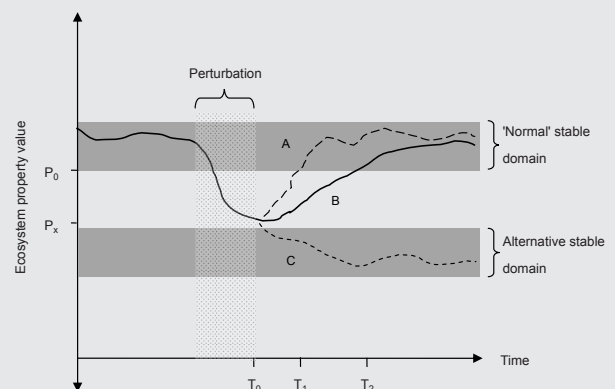


Figure 1. Concepts of engineering and ecological resilience in ecosystems. A system with greater engineering resilience (A, long dash line) would have a shorter return-time interval ($T_1 - T_0$) compared with a system with lesser engineering resilience (B, solid line) with a longer return-time interval ($T_2 - T_0$) following perturbation of a system property from P_0 to P_x . A system with greater ecological resilience (A or B) will return to the 'normal' stable domain following a perturbation of the system property from P_0 to P_x compared with a system with lesser ecological resilience (C, short dash line) that enters an alternative stable domain following a perturbation of the same magnitude, having crossed a hysteresis-type threshold between P_0 and P_x .

Approach

We used two approaches to explore resilience, the first based on a consensus model of forest fragment system dynamics developed by a team of ecosystem scientists and the second based on empirical data generated in the ‘Forest fragment resilience’ research project (Innes 2009), supplemented by other information on forest fragment disturbance dynamics gleaned from the literature.

Our evidential basis for drawing conclusions about the relative resilience of forest fragments requires first that they show a significant response of key system properties to the perturbations of interest (grazing and mammalian pests). This immediately highlights the issue of how to define the initial conditions, in the absence of fragments that have never been grazed or infested with weeds and pests. Studies to date have used larger forest tracts, but two difficulties are apparent: (1) the fact that the reference forests are not fragmented, and thus any fragmentation-specific effects or interactions will not be expressed, e.g. species–area relationships, dispersal limitations; and (2) the idiosyncratic management of most reference forests, in terms of which mammalian pests and weeds are controlled and over what time period. Despite these limitations, reference forests represent a major resource for our ability to infer initial conditions, guided by our growing understanding of the historical condition and dynamics of indigenous forest ecosystems. Hence in this study we also cautiously use reference forests to inform our assessment of resilience, focusing on high-level indicators to minimise the associated uncertainty.

Having established the existence of perturbation effects, relative engineering resilience would be indicated by the extent to which system properties show a return response following release from those perturbations, over the timescales encompassed by the data (one or two decades): high engineering resilience is indicated by full recovery and low engineering resilience is indicated by partial recovery (cases A and B in Fig. 1). By contrast, relative ecological resilience would be indicated by the occurrence of a return response to release from the perturbations along with changes in system controls (as indicated by the feedback loops described below): high ecological resilience is indicated by a full or partial recovery and low ecological resilience is indicated by a lack of recovery after multiple decades accompanied by changes in system controls (case C in Fig. 1). Such changes in system controls should distinguish low ecological resilience from low engineering resilience when observing very slow recovery.

System dynamics model

We developed a system model of forest fragments using the causal loop diagram approach from the discipline of system dynamics (Maani & Cavana 2007). The rationale for using this approach is that an explicit documentation of the dynamics of the ecosystem should: (a) help integrate our understanding of key ecosystem processes across different ecosystem components (plants, invertebrates, soils, mesofauna); (b) highlight the most important structural and functional parameters of the ecosystem to guide measurement and monitoring; and (c) reveal a number of features of system behaviour that are relevant to analysing resilience, specifically the nature of any feedback loops.

Within the system dynamics framework, we identified key system variables and depicted the nature of the relationships between those variables with annotated arrows. The direction of the arrow indicates a cause–effect relationship, while the

annotation indicates the direction of the effect, thus: + represents a positive effect (i.e. both variables increase together or both variables decrease together) and – represents a negative effect (i.e. one variable increases while the other decreases). Within this system diagram we identified the feedback loops, of which there are two types:

- (1) Reinforcing loops (R), whereby the feedback is positive overall (when multiplying the signs of the annotations) and results in enhancement of the initial change in the key variable, also called a ‘vicious’ or ‘virtuous’ cycle.
- (2) Balancing loops (B), whereby the feedback is negative overall and results in moderation of the initial change in the key variable.

The system model was initially built for a ‘natural’ system, excluding the role of the major human-mediated perturbations of interest (livestock grazing, pest invasion). The relevant perturbations were then considered in terms of whether they modified the system state variables, modified the nature of the feedback loops, or added new feedbacks (see Fig. 2).

Experimental data

Forty-seven low altitude forest fragments in the Waikato Region, ranging in area from 0.5 to 24 ha, were surveyed during the summer of 2006/07 (for details see Didham et al. 2009; Burns et al. in press). The fragments were selected according to distinct historical management regimes of fencing to exclude livestock and pest control, arranged in a factorial design. This arrangement included four categories of fencing: unfenced or fenced <2 years; fenced 2–10 years; fenced 10–20 years; and fenced >20 years) and two categories of pest control targeted at possums (*Trichosurus vulpecula*) and ship rats (*Rattus rattus*): uncontrolled and controlled – the latter defined as being conducted for a minimum of 2 years and usually > 10 years, with at least annual repeats at a minimum of one trap or bait station per hectare.

Data on vascular plant structure, plant species composition and soil characteristics were collected from a subset (41) of tawa (*Beilschmiedia tawa*) dominated forest fragments (Burns et al. in press). Data on forest-floor invertebrate faunal composition and site characteristics were also collected from a subset (30) of the fragments (Didham et al. 2009). Bird nesting success using real and model nests was assessed in fragments with and without intensive ship rat and possum control, and ship rat abundance was measured in fragments with and without grazing (Innes et al. 2010b). Corresponding data were collected from, or obtained for, three large local forest reserves (Te Miro, Karakari and Maungatautari scenic reserves), all of which were free of livestock but which have had only limited recent mammalian pest control. Key ecosystem variables incorporated into the system dynamics model were selected from the plant, soil, invertebrate and bird data, which were transformed into semi-quantitative values (i.e. nil–low–medium–high). These values were compared with estimates of the ‘normal domain’ from the field studies and other available literature. This comparison aimed to examine the system’s responses to removal of livestock and pest mammal perturbations, and to determine if the measured responses provided evidence of engineering and/or ecological resilience.

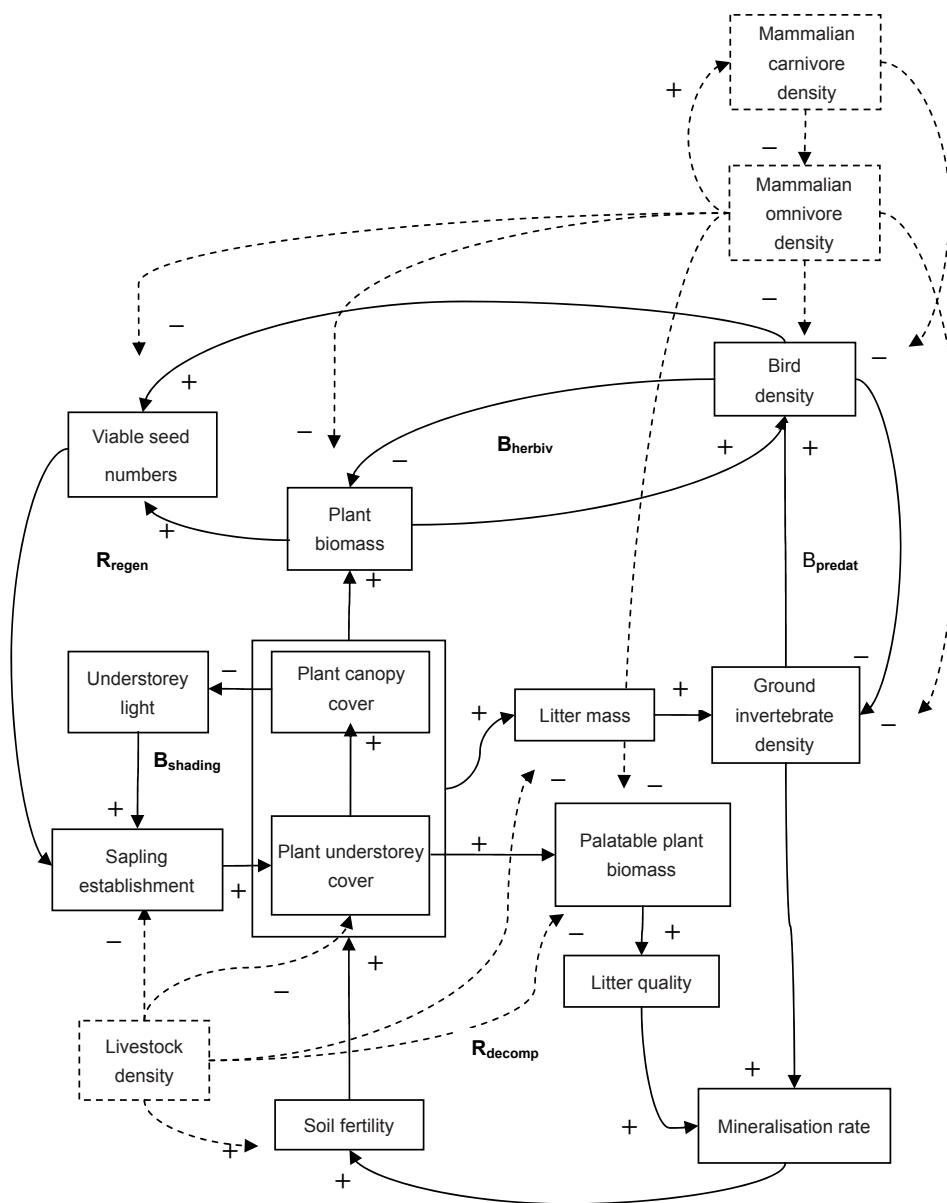


Figure 2. Causal-loop system dynamics model of a forest fragment ecosystem showing key reinforcing loops (regeneration, R_{regen} ; decomposition, R_{decomp}) and balancing loops (shading, $B_{shading}$; herbivory, B_{herbiv} ; predation, B_{predat}). New structure created by the perturbations of interest is shown by dashed boxes and arrows indicating major direct effects. Symbols: + positive effect; - negative effect.

Results and discussion

System dynamics model

The quite complex initial cause-and-effect diagrams were simplified to include only the key causal loops identified as major controls (Fig. 2). Two linked clusters of reinforcing and balancing loops were evident. The first cluster was based around plant growth and regeneration. The reinforcing component of this pair involves the standing vegetation biomass generating current seed production, which germinates under favourable conditions, leading to regeneration of saplings in the understorey (Fig. 2). These saplings contribute initially to understorey cover but also via a slowly operating process to canopy cover (for the relevant canopy species, i.e. tawa and rewarewa – *Knightia excelsa*). A component of those favourable conditions is the light environment under the canopy, which provides the balancing control on sapling regeneration. The consumption of leaves and flowers, predominantly by avian herbivores, in pre-disturbance New Zealand ecosystems (Clout

& Hay 1989) also provides a balancing loop that checks plant growth and perhaps regeneration, but native birds are also crucial pollinators and fruit dispersers (Kelly et al. 2006) and so are necessary for plant regeneration.

The second cluster of reinforcing and balancing loops was based around resource-consumer interactions and decomposition processes (Fig. 2). The first reinforcing component of this pair involves the standing vegetation biomass generating leaf litter, which is decomposed by the invertebrate community, thereby recycling nutrients for plant growth. The second reinforcing component consists of the suite of relatively palatable plants associated with understorey cover, which increases litter quality and influences mineralisation rates (Pastor et al. 1993). The linked balancing control on this process is the predation of the macroinvertebrate community by the avifauna. The plant regeneration balancing loop also provides a long-term control on plant biomass and litter production.

The direct effects of the two perturbations of interest in the

initial model are outlined in the dashed boxes and arrows in Fig. 2. Livestock browsing can be a pulse or press disturbance, but in the context of most New Zealand farm systems it involves rotationally grazed livestock having access for repeated short periods (e.g. wintering cattle) and thus should be regarded as a press disturbance. Livestock have several impacts on forest fragments, including removal of the understorey vegetation (particularly the most palatable plants) by direct browsing, suppression of sapling regeneration by direct browsing and physical damage of seedlings by trampling (Jane 1983; Timmins 2002), introduction of adventive species through propagule transport from the pastoral matrix (with likely enhancement of establishment through soil disturbance) and elevated nutrient supply (via faeces and urine). Overall, these impacts serve to weaken the plant growth and regeneration reinforcing loop by damage to seedlings and saplings, while at the same time strengthening the herbivory balancing loop by addition of herbivore consumption of foliage and strengthening the soil fertility loop by addition of nutrients in dung and urine. This direct effect may serve to offset negative effects on the decomposition loop (see Wardle et al. 2001). However, it was considered that the inclusion of livestock in the model did not create any new reinforcing or balancing loops within the system.

Livestock impacts

Livestock browsing is not analogous to that of indigenous herbivore browsing in unperturbed systems. Because livestock are primarily fed on the pastures surrounding forest fragments, and their numbers are determined by the farm manager, there is no balancing feedback loop to control their population and their rate of consumption of forest fragment vegetation, as is the case for native herbivores (Fig. 2). This external resource subsidy effect creates the potential to push the system into a new domain, through ongoing prevention of the recruitment of canopy trees. At some point the existing trees will die through natural attrition and the structure of the forest might change sufficiently such that removal of the livestock will not result in a return to a pre-grazed state, which would be a case of a regime shift to an alternative state (Box 1). It is thus valuable to know for how long a forest fragment can be grazed by livestock before this shift occurs. This period could be an empirical measure of the ecological resilience of the forest fragment to livestock grazing (i.e. the temporal magnitude of the disturbance required to force the regime shift, sensu Holling 1996). We predict that the time frame of this process would be related to the longevity of the dominant canopy species, which for tawa is in the order of 300-plus years (West 1995).

In terms of empirical evidence for this process, Esler (1978, p. 45) documents the degeneration of indigenous forest fragments induced by long-term browsing and characterises it as a three-stage process of understorey destruction, weed infestation and finally canopy collapse, leaving only scattered former subcanopy trees in a grassland matrix. On the other hand, Esler (1978, pp. 73–77) also describes forest regeneration via bracken/mānuka/gorse shrubland succession, resulting from decreasing grazing intensity in steep sown grassland. In mesic environments, vegetation often shows classical secondary succession through shrubland to indigenous-dominant forest over timescales of decades (McQueen 1993; Leathwick & Rogers 1996; Sullivan et al. 2007) to centuries (as modelled by Meurk & Hall 2006). Thus even in this case of complete deforestation in mesic regions of New Zealand, an engineering resilience framework may still be appropriate, since even

forest destruction may not represent a permanent regime shift. Given the generally poor representation of native plant seed in non-forest soils (Partridge 1989) and the absence of persistent seed banks (Sem & Enright 1996; Moles et al. 2000), the local availability of dispersed propagules from remaining forest and the continuity of the associated dispersal mechanisms will be important factors in forest regeneration from grassland (Meurk & Hall 2006; Standish et al. 2009). Hence the climate and landscape context of the forest fragment becomes an important mediating factor in determining resilience.

Mammalian pest impacts

The impact of mammalian pests can also be considered as a press disturbance in terms of the ubiquitous build-up and ongoing maintenance of high pest populations in the vicinity of all fragments (Batcheler & Cowan 1988; King 2005). As with livestock, individual pest species (e.g. possums, ship rats) can have multiple impacts on structural and functional components of the system, which can be exacerbated by the occurrence of a suite of pest species with multiple functional roles. This is illustrated in Fig. 2 by the inclusion of two new state variables representing mammalian omnivores and predators. It is worth noting that while predation of birds would have been a feature of natural systems, we did not regard this as a dominant control on bird populations (Innes et al. 2010a), and hence indigenous predation was omitted from Fig. 2. Mammalian pests that are omnivores (possums, ship rats and mice *Mus musculus*) have direct negative impacts on flora, though on different system variables than those identified for livestock impacts. Thus pest mammal impacts also weaken the growth and regeneration reinforcing loop by consumption of seeds and seedlings and strengthen the herbivory balancing loop by additional herbivore consumption of foliage throughout the canopy layers. Many omnivorous pests (particularly hedgehogs *Erinaceus europaeus*) are also predators of invertebrates, potentially weakening the decomposition reinforcing loop. Thus, they are engaged in the herbivory and invertebrate predation loops in the same manner as indigenous birds (i.e. as competitors; Nugent et al. 2000; McQueen & Lawrence 2008). However, two of these omnivorous mammalian pests (possums and ship rats) are also direct predators of indigenous birds (via nest predation; Innes et al. 2004) and hence operate as joint competitors and predators. Furthermore, they are also prey items themselves (along with birds) for the introduced mammalian predators (e.g. stoats *Mustela erminea*) and thus create an important new predation balancing loop, whereby the mammalian omnivores support a mammalian predator population that can prey-switch between the mammalian omnivores and the indigenous bird population (Murphy et al. 2008). Overall, the inclusion of this suite of mammalian pests represents a new and quite complex dynamic in the forest fragment ecosystem, which has two major detrimental aspects for the avifauna, which we term the competitor-predator effect and the predator-support effect.

The importance of external resource subsidies noted previously for livestock grazing effects is also relevant for pest mammals to a large extent, since they typically range widely and have access to numerous food resources in the wider non-forest landscape. For example, a substantial component of possum diet appears to be high quality pasture in agricultural landscapes (Harvie 1973; Nugent et al. 2000; Dodd et al. 2006). Consequently the populations of both livestock and pest mammals that inhabit forest fragments are not subject solely to internal balancing feedback controls within the

fragment, but also to the destabilising influence of external resource subsidies.

Resilience in the system model

The question of whether the model has any characteristics that support the concepts of engineering and/or ecosystem resilience can be addressed by considering what the model might qualitatively predict following the release from livestock and pest mammal perturbations, through management actions such as fencing and pest control.

In the case of livestock browsing, our model indicates that this perturbation functions within the context of existing feedback loops (the reinforcing regeneration loop, and the balancing shading and herbivory loops). This suggests that the growth reinforcing loop will continue to function following removal of the perturbation, leading to recovery of the vegetative structure of the forest. Therefore, exclusion of livestock browsing by fencing should lead to fairly rapid recovery of sapling regeneration and understorey cover, with slower effects on soil fertility (as elevated nutrients dissipate) and plant diversity (as adventive herbaceous species become subject to control by the shading loop). The lack of permanent changes in system structure and feedback control due to livestock browsing suggests that the fragment will exhibit a release response in these variables that is characteristic of relatively high engineering resilience. However, fencing in the absence of pest control leaves open the question of whether the weakening of the regeneration loop due to flower, fruit and seed herbivory by mammalian omnivores will inhibit understorey sapling regeneration in the medium term and thus result in a decline in canopy cover in the longer term.

The effects of pest mammal control will be dependent on which pests are controlled. Elimination of carnivores (stoats and feral cats *Felis catus*) may have little positive impact on the forest fragment, because of their mainly indirect effects and low densities (often only 1–2 per 100 ha or fewer). Carnivore removal may even exacerbate damage by omnivorous rodents that are no longer subject to this balancing control, thus ensuring there will effectively be no release from perturbation. By contrast, the removal of the mammalian omnivores should result in fairly rapid recovery of plant regeneration and invertebrate populations, but will not necessarily benefit the avifauna while mammalian carnivores remain in the local environment. A particular feature of the system is that there is no balancing feedback from bird populations to either the carnivore or omnivore mammal guilds (i.e. there is no reduction in food supply resulting from predation that would normally make either guild food-limited), since the omnivores (ship rats, possums, mice) also eat fruit, seeds, leaves and invertebrates and the carnivores (stoats, cats) also eat other mammals. Thus, either guild has the potential to drive the birds to extremely low population levels without any density-dependent feedbacks. The resultant wholesale replacement of this important component of the indigenous herbivores with an introduced fauna could well constitute a ‘regime shift’ in the language of ecological resilience. It is thus possible to envisage a release response characteristic of engineering resilience in components of the system (plants and invertebrates), but no response in other components (birds) as evidence of a lack of ecological resilience.

In summary, comparing the system dynamic effects of livestock and mammalian pests leads to the conclusion that both have extensive networks of impacts that ramify throughout the system, which serves to emphasise the devastating effect

they have on lowland forest fragments. However, each operates largely on different components of the system, which tends to suggest (1) that the combination of both perturbations will be far more detrimental to the whole system than either one operating alone, and (2) that release from one or other of the perturbations will have differential effects, leading to differing restoration endpoints and possibly alternative stable domains.

Empirical data

The system dynamics model indicated that a number of key ecosystem variables would provide information on dynamic responses to perturbation release, particularly with respect to plant regeneration, plant canopy cover, palatable plant biomass, litter mass, litter decomposition rate, invertebrate density, soil fertility and bird populations. The semi-quantitative data derived from the empirical data in the forest fragment resilience study (Didham et al. 2009; Burns et al. in press), with quantitative approximations, are shown in Table 1.

The data confirm the substantial effects of perturbation by livestock grazing and mammalian pests on key indicators of ecosystem structure in forest fragments relative to ungrazed reference forest systems. Specific effects include declines in plant regeneration (low seedling and very low sapling numbers), palatable plant cover, invertebrate density, litter mass and decomposition rate and increases in soil fertility (lower soil C:N). These patterns are also reflected in other data from the limited literature on the ecological condition of forest fragments in New Zealand. For example Smale et al. (2008) and Dodd and Power (2007) have also shown inhibited regeneration and low litter cover in grazed fragments. With regard to soils, Stevenson (2004) has shown high levels of inorganic phosphorus, but no differences in C and N, in forest fragments compared with ungrazed forests. Soil-fertility-related properties appear to be highly variable between forest fragments, reflecting localised fertiliser and stock management. In mid-elevation *Nothofagus* forests in the South Island, Ewers et al. (2007) and Ewers and Didham (2008) found that beetle community structure was dramatically altered in small forest fragments and at the edges of large forests, relative to interior forest sites, with the loss of some interior forest specialists (Ewers & Didham 2004). Bird nesting success is low in *both* large reference forests and small fragments due to the ubiquitous distribution of pest mammals (King 2005), although food shortage due to inadequate habitat area is undoubtedly an additional problem for native birds in fragmented landscapes (Innes et al. 2010a).

Resilience in the data

All of the indicators in Table 1 show return behaviour with release of the fragments from either livestock grazing or mammalian pest impacts. Some show a ‘full’ recovery – seedling and sapling densities recover with fencing, invertebrate densities recover with both fencing and pest control. Others show a ‘partial’ recovery – canopy cover increases with pest control, litter mass increases with fencing, soil C:N increases with fencing. Partial recovery may simply be a function of time, where feedback cycles operate over long periods and thus rates of change are slow (e.g. soil C:N as a function of litter return and decomposition). It may also be a function of the incomplete nature of the perturbation release (e.g. only possum and rat predation of invertebrates is controlled). Some variables show no recovery, consistent with a lack of direct relationship as indicated by the system dynamics model (e.g.

Table 1. Semi-quantitative dynamics of forest fragment ecosystem variables in reference forest, perturbed fragments and fragments in response to long-term fencing and mammalian pest control, with approximations of the semi-quantitative variables based on field data (from Dodd et al. 2009; Innes et al. 2010b; Burns et al. in press). DW = dry weight; C:N = carbon:nitrogen.

System variable	Indicator variable	Units	Low	Medium	High	Reference forest	Perturbed fragment	With fencing	With pest control	With both
Plant regeneration	Seedling density	stems m ⁻²	100	1000	10000	Medium–high	Low–medium	Medium–high	Medium	Medium–high
Plant regeneration	Sapling density	stems m ⁻²	10	100	1000	High	Nil–low	Medium–high	Nil–low	Medium–high
Canopy cover	Cover of canopy species	% cover	70	80	90	High	Medium	Medium	Medium–high	Medium–high
Palatable plant biomass	Palatable plant cover	% cover of defined spp. ¹	5	10	20	High	Nil–low	Medium–high	Low	High
Decomposition rate	Litter bag mass loss	% mass loss over 200 days	40	60	80	Medium	Low	Medium	Low	Medium
Litter mass	Litter mass	t DW ha ⁻¹	6	8	12	High	Low	Medium	Low	Medium
Invertebrate density	Ground invertebrate density	number m ⁻²	500	1000	2000	High	Low	Low–medium	Medium	High
Soil fertility	C:N ratio	n/a	10	15	20	Medium–high ²	Low–high ²	Medium	Low–medium	Medium
Bird density	Bird nesting success	% nests that fledge young	20	40	60	Low ³	Low	Low	High	High

¹Palatable species include *Asplenium bulbiferum*, *Coprosma grandifolia*, *Cyathea medullaris*, *Geniostoma rupestre*, *Schefflera digitata*.

²See Sparling & Schipper (2002).

³See Innes et al. (2010a).

sapling density is unaffected by pest control, invertebrate density is minimally affected by fencing).

Other studies in the New Zealand plant ecology literature confirm this general picture of partial recovery in system attributes following removal of the agents of perturbation. Paired browser-exclusion plot studies have shown recovery of palatable plant species (Smale et al. 1995; Husheer et al. 2005), though the effects have not been consistent, leading to a number of hypotheses for non-recovery (Coomes et al. 2003). While we know of no published studies of the temporal sequence of recovery of New Zealand forest fragments following the alleviation of disturbance, two studies of forest fragment vegetation have used a space-for-time substitution approach to study recovery after the exclusion of domestic livestock. One study was in lowland kahikatea (*Dacrycarpus dacrydioides*) fragments (Smale et al. 2005) and the other in lowland tawa fragments (Dodd & Power 2007). In these studies, several fragments with differing periods of time since fencing were assessed for vegetation and soil characteristics. This approach implicitly follows an engineering resilience paradigm, i.e. the equilibrium domain is assumed to be a forest where the browsing disturbance was not present. The (spatially simulated) changes in structure and composition of the fragments over time frames of 10–20 years since grazing exclusion in Smale et al. (2005) and Dodd & Power (2007) included increases in sapling regeneration / understorey cover and decreases in soil P fertility, consistent with a view of

the soil and vegetation component of forest fragment plant communities being resilient to livestock browsing.

In the only nest survival study undertaken in New Zealand fragments so far, Boulton et al. (2008) found that robin (*Petroica longipes*) nest survival ‘marginally decreased’ with fragment size. While nest survival is generally poor in both small and large forests, it can be increased methodically in either with predator control (e.g. Innes et al. 1999, 2004; studies summarised in Innes et al. 2010a). Rare species may have to be restored to fragments by translocation. The short-term absence of these species from fragments despite pest control could be viewed as an example of a lack of ecological resilience, but other species have recently been demonstrated to establish new populations in reserves independent of translocations (Miskelly et al. 2005), which may then be evidence for engineering resilience on a longer timescale, and requiring a larger spatial scale of pest management (e.g. Basse & McLennan 2003) focused on many rather than single fragments.

The experimental data also revealed unexpected interactions between components of the model. Ship rats were significantly more abundant in fenced than in grazed fragments, probably due to the higher biomass of vegetation, fruits and seeds, and litter invertebrates. In this sense, ship rats simply replace native birds in Fig. 2 in terms of responding to the abundance of flowers, fruit and seed and supplying a balancing loop that reduces flower, fruit and seed abundance. However, ship rats cannot replace native birds as effective agents of

flower pollination and seed and fruit dispersal (Williams et al. 2000; Kelly et al. 2006).

Overall, with respect to our objectives, we suggest that the data present a picture of generally high ecological resilience (no evidence of a lack of recovery over decadal timescales) but variable degrees of engineering resilience for different components of the forest fragment ecosystem (differing recovery rates). Specifically, the vegetation and invertebrate components show high engineering resilience, while the soil and bird components show lower engineering resilience. Bird fauna show the potential for a lack of ecological resilience (no recovery and changes in system controls), although firm conclusions are obscured by lack of data. Thus the engineering resilience paradigm appears to be an adequate model to inform restoration. However, we emphasise that this assessment is restricted to fragments in mesic environments, to landscapes with good opportunities for immigration (i.e. fragmented but not relictual), and to fragments impacted by livestock and pest mammals over timescales of multiple decades.

Developing a management framework

One of the key questions that we sought to address from this work is 'What are the implications of our systems understanding for the future management of forest fragments in New Zealand?' Fundamentally, management works through a process of developing goals and objectives; developing supporting indicators and assessing the current state of a system relative to management goals; applying management actions that have a reasonable expectation of making progress toward the goals; and monitoring outcomes using the same set of indicators. Our results can inform all of these stages to varying degrees:

Goals

A key issue is that of setting appropriate goals for managing forest fragments, and perhaps the most important message from the study reported here is that the use of large ungrazed and pest-controlled forest systems as a benchmark for restoration is not entirely appropriate, given (a) that for some variables, long-term fencing and pest control have not led to conditions similar to 'reference forests'; (b) known effects of area and fragmentation on species richness (Hobbs & Saunders 1994; Lomolino 2000); and (c) tentative evidence of the inability of some species to recolonise areas after disturbance release. Given that the prevailing agricultural land-use matrix over much of New Zealand is unlikely to change in the foreseeable future, many of the drivers of disturbance will remain present in the current landscape context indefinitely (Norton 2009). The well-recognised effects of this (i.e. permanent loss of area-sensitive species, reduction in potential species richness, and loss of dispersal mechanisms) imply a need for rethinking of the goals of restoration (Hobbs & Harris 2001). At the very least we must seek goals that reflect reasonable targets for fragmented ecosystems. Such goals may discard a restoration paradigm in favour of a reconstruction paradigm that focuses on ecosystem goods and services rather than biotic history (Jackson & Hobbs 2009).

Indicators

The development of a system dynamics model and the process of refining it to depict the key variables (pools and/or processes) highlights the most useful parameters for assessment and monitoring of forest fragment condition. Measurement of canopy cover, plant biomass, plant reproduction (flower/

fruit/seed and saplings), understorey cover, understorey light, litter mass, invertebrate density, plant diversity, litter quality, mineralisation rate, soil fertility, and bird populations within a forest fragment should give a clear indication of the structural and functional integrity of the ecosystem. However, even this limited set of indicators is likely to be too onerous for most land managers to measure or monitor, suggesting that there will be a strong need for further refinement of key indicators. The system dynamics model would suggest that a minimal set of indicators comprises the parameters that capture the operation of the major causal loops, namely: understorey light (the balancing shading loop); sapling numbers (the reinforcing regeneration loop); litter mass (the reinforcing decomposition loop); and bird numbers (the balancing herbivory and predation loops) (Fig. 2). All have specific methods of visual or aural assessment that are relatively inexpensive and require minimal training.

Actions

Assuming that an assessment of the condition of a forest fragment identifies a mismatch between current and desired state, the manager will probably want to know the extent to which s/he can rely on natural processes versus the need for active intervention to achieve the desired result. Our results indicate that if the manager wishes to restore plant species diversity and understorey regeneration, we can confidently advise that putting up a livestock-proof fence will achieve this goal, as the understorey flora will recover without the need for supplementary planting. This conclusion is based on our assessment of the relative resilience of the indigenous understorey flora to livestock browsing, but may not be true for canopy structure and composition. If the manager wishes to restore macroinvertebrate fauna, we may advise that stock fencing or elimination of mammalian omnivores alone will have limited value, and both are required (Didham et al. 2009). This is based on our assessment of the relative resilience of the indigenous invertebrate fauna to the combination of stock browsing and mammalian predation. If the manager wishes to restore nesting native bird populations, we may advise that even complete control of mammalian fauna will not be sufficient alone, and some form of reintroduction of bird species will be required. This is based on our assessment of the relative lack of resilience of the indigenous avifauna to mammalian predation/competition. The latter example represents a key dividing line between management by perturbation release (which relies on the engineering resilience of the ecosystem to restore structure and function) and management by ecosystem reconstruction (which accounts for the lack of ecological resilience and seeks to rebuild the system as well as protect it from further perturbation).

Monitoring

Given that the manager will also be interested in the likely time frame over which s/he can expect to observe an improvement in fragment condition following fencing and pest control, the results can suggest appropriate monitoring intervals for the key indicators outlined above. Based on the limited studies available to date, measurable changes should be apparent after 0–5 years for litter mass, 5–10 years for plant diversity and bird numbers, 5–15 years for sapling numbers and >20 years for understorey light levels.

A conceptual management model

Finally, we sought to develop a conceptual management model at the fragment scale that could incorporate the concepts of resilience discussed in this paper with the more familiar concepts of forest condition and ecosystem integrity. Our conclusion about the adequacy of an engineering resilience paradigm for our system of interest suggested that a linear framework with few indicator variables would be adequate, so long as it could incorporate threshold dynamics where evidence for them emerged. Lee et al. (2005) have suggested three indices of integrity for cross-scale biodiversity inventory and monitoring by the New Zealand Department of Conservation: (1) 'Indigenous dominance' (the level of indigenous species' influence on the structure and function of ecosystems); (2) 'Species occupancy' (the extent to which the indigenous species capable of living in an ecosystem are present); and (3) 'Environmental representation' (the distribution of indigenous ecosystems across environmental gradients).

We have drawn on the indices of Lee et al. (2005) to develop a conceptual management model for forest fragments, by first creating a semi-quantitative empirical example (Fig. 3) and then formulating a generalised model (Fig. 4). The model incorporates a two-dimensional 'state-space', akin to the restoration scenarios depicted in Suding et al. (2004, Fig. 2) to reflect the condition and dynamics of forest fragments in the context of associated ecosystems. At the scale of individual forest fragments that we are interested in here, environmental representation is less relevant to fragment management, so we have focused on the first two indices of Lee et al. (2005), with some modifications outlined below.

From the terms described by Lee et al. (2005), we have modified the terminology of the second index to 'community occupancy' to distinguish it from other definitions of species occupancy that focus on spatial abundance (e.g. MacKenzie

et al. 2005). In addition, it is likely that the structural component of an indigenous dominance index (in particular species composition) will be highly correlated with an occupancy index, so we have focused the *x*-axis of our two-dimensional state-space on the combination of these two components (which we call indigenous community occupancy), and we focus the *y*-axis of the state-space solely on the functional component of indigenous dominance of ecosystem processes (which we call indigenous functional dominance).

Semi-quantitative example

Figure 3 populates the state-space using data from the Smale et al. (2008) study, along with more recent data from the same Whatawhata site in the western Waikato hill country (MBD, unpubl. data). These data provide the basis for an analysis using vascular plant data from forest ecosystems under five different management regimes: the interior of a large reference forest, the interior of a grazed and pest-infested forest fragment, the edge of a grazed and pest-infested forest fragment, the interior of a small fragment fenced and pest controlled for 7 years, and the edge of a grazed and pest-infested forest fragment fenced for c. 40 years. The use of vegetation data only, rather than a more complete analysis including faunal data, reflects the relative availability of this information. The compilation of a list of extant indigenous species from which to estimate indigenous community occupancy is simple, but determining the denominator for calculating percent occupancy relative to the Lee et al. (2005) criteria that 'indigenous species capable of living in an ecosystem are present' is less straightforward. In this case we have used the mean number of indigenous species (85) identified in an 800-m² area of reference forest from fig. 2 of Smale et al. (2008), on the basis that this represents the approximate spatial scale of the measurements from the grazed fragments in that study. The general lack of

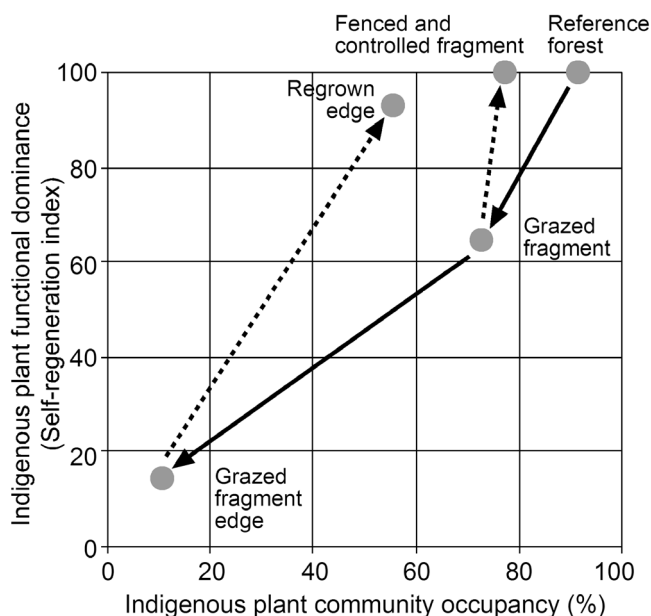


Figure 3. Semi-quantitative dynamics of plant communities in forest fragment ecosystems in response to livestock grazing and mammal pest invasion (solid arrows), and the release from these press disturbances at two stages of degradation (dashed arrows). Data based on Smale et al. (2008) and subsequent unpublished data from that study site.

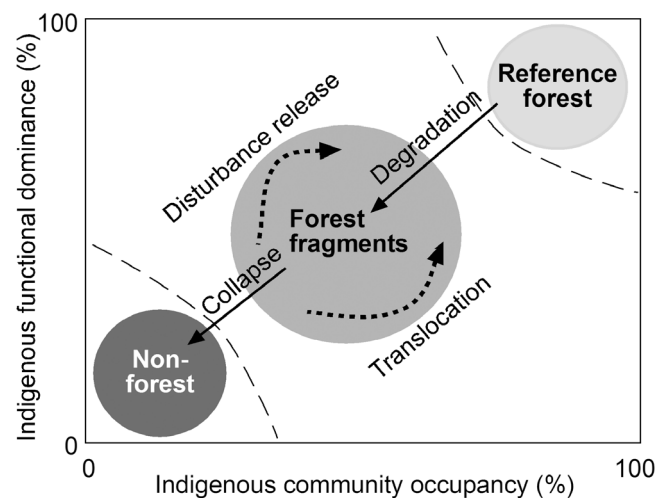


Figure 4. A conceptual state-space for forest fragment ecosystems, based on indigenous functional dominance and indigenous community occupancy, showing the major recognisable states of extant forest (light grey), forest fragments (mid-grey) and non-forest or forest edge (dark grey); observable trajectories of degradation (solid lines) and recovery (short-dash lines); and potential thresholds associated with fragmentation and collapse (long-dash lines).

baseline information on historical species distributions in New Zealand represents a major limitation to the development of management goals and indicators. For canopy tree species, a potential natural vegetation layer has been constructed for vegetation composition in New Zealand prior to the arrival of humans (Leathwick 2001), but similar reference points for floral or faunal composition are not available for the vast majority of taxa.

In generating the data for the y-axis (indigenous functional dominance) of Fig. 3, we note that Lee et al (2005, p. 107) state 'The cornerstone of continued indigenous dominance is self-regeneration...'. Therefore we chose to plot functional dominance in terms of the juvenile abundance of indigenous species, using a three-stage scoring system (nil = 0; low = 1; high = 2). We have assumed that all non-woody species with lifespans less than the period of livestock grazing or mammalian pest disturbance must have successfully regenerated under these conditions (i.e. score = 2) and based the score for longer-lived woody species on sapling abundance. The self-regeneration index is the sum of the juvenile abundance scores divided by the number of indigenous species present as adults ($\times 2$), converted to a percentage ($\times 100$). This simplistic approach has some obvious weaknesses (e.g. how to account for the observation that even when all juveniles are indigenous species the juvenile population may not encompass the full range of adult species occupying the site, due to stochastic reproduction or dispersal failure; and how to account for juveniles dispersing into plots where no adults are present) but further development of this index is beyond the scope of the illustrative discussion in this paper.

Based on this semi-quantitative worked example (Fig. 3), there is a clear distinction in both indigenous community occupancy and indigenous functional dominance between the reference forest and the interior of a degraded forest fragment. There appear to be two alternative trajectories that the forest fragment ecosystems at this site have followed, corresponding to either improvement in indigenous species occupancy and functional dominance associated with the recovery of a forest fragment released from livestock grazing and pest mammal impacts, or further degradation to very low levels of indigenous community occupancy and functional dominance that might be reflected in current state observed in fragment-edge environments, which have few remnant canopy trees and consist primarily of tree ferns and adventive weeds. The data from the long-term fenced remnant edge indicate substantial recovery in both occupancy and dominance from even this highly degraded state.

The semi-quantitative model of plant community dynamics in Waikato forest fragments (Fig. 3) can be generalised to other components of the structure and functioning of forest fragment ecosystems throughout lowland areas of New Zealand (Fig. 4). In this general conceptual model, we note that the reference forests to which the condition of forest fragments are often compared (large tracts of indigenous forests in which some degree of conservation management has occurred) do not occupy the extreme top right 'pristine' space in the diagram (Fig. 4), due to species extinctions, associated loss in ecosystem function, and the influence of exotic weeds and pests on ecosystem processes. We also note that non-forest ecosystems (e.g. pastoral land) do not occupy the extreme bottom left 'completely degraded' space in the diagram (Fig. 4), since these habitats commonly contain some indigenous species that can have a significant contribution to ecosystem processes (e.g. grass grub beetle *Costelytra zealandica*, and meadow ricegrass

Microlaena stipoides). Nevertheless, it is clear that the reference forests would be regarded as having relatively high ecological integrity, while pasture would be regarded as having relatively low ecological integrity, from the point of view of retaining the 'natural character' of indigenous ecosystems. Between these two extremes of indigenous occupancy and functional dominance, there are likely to be a range of degradation and recovery pathways through which ecosystems might be forced, but all the degraded forest fragments considered here appear to occupy the central space in the diagram (Fig. 4).

The process of human-mediated restoration generally involves two approaches: (1) disturbance release (e.g. fencing, pest control), which focuses on restoring the indigenous functional dominance and which by itself implicitly assumes spontaneous immigration and improvement of community occupancy; and (2) translocation (e.g. tree planting, reintroducing birds), which focuses on restoring community occupancy and which by itself implicitly assumes the presence of these species will improve indigenous functional dominance. Thus, recovery of ecosystem integrity is represented by an upward and/or rightward shift in Fig. 4. The rate or extent to which this occurs can be considered a measure of engineering resilience.

Summary

It is of particular interest whether forest fragment recovery processes are inhibited by the existence of thresholds, since this would have a bearing on the likelihood of restoration failure following management intervention. A lack of evidence for thresholds and associated positive feedback loops operating within a system would suggest that an engineering resilience paradigm might be adequate for management purposes. Under this model, it would be reasonable to expect that mitigation of adverse drivers would lead to an upward and rightward shift (i.e. successful recovery) of the forest fragment system. The results of the studies reported here indicate that this is the case. We did not find strong evidence for a lack of ecological resilience in the empirical data (Table 1, Fig. 3a). However, the system dynamics model did suggest that low ecological resilience may be an issue in respect of the avifauna and mammalian pest effects. In addition, the scope of our study was confined to already fragmented ecosystems, and further exploration of the specific effects of the fragmentation process might provide evidence of a lack of ecosystem resilience in lowland forest fragments to historical human impacts.

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