

Clear-fell harvest impacts on biodiversity: past research and the search for harvest size thresholds

S.M. Pawson, E.G. Brockerhoff, D.A. Norton, and R.K. Didham

Abstract: Clear-fell harvesting has large aesthetic impacts and significantly alters ecosystem attributes at multiple spatial scales. Known abiotic changes include increased microclimatic variability, changes in regional water balance, and modified hydrological patterns that influence erosion processes. Biotic changes include increased species richness immediately post-clear-felling due to shifts in species composition resulting from changes in individual species abundance and colonization by disturbance-adapted or open-habitat species. Given the large ecological changes caused by clear-fell harvesting and the negative public perception of clear-felling, it is surprising that few studies have investigated whether reducing clear-fell harvest area may be a viable strategy to mitigate ecological change within individual clearcuts. Clear-fell size studies conducted to date rarely exceed a maximum harvest area of 10 ha, and biotic communities measured exhibit mixed responses with respect to species richness and other biodiversity attributes with increasing clear-fell size. Some postharvest ecological responses are nonlinear with respect to harvest area and suggest possible threshold sizes beyond which clear-fell impacts increase disproportionately to their size. Conceptual models of potential ecological thresholds in clear-fell harvest impacts are discussed, as is the need for rigorous empirical testing to ensure a solid foundation exists for forest harvesting guidelines.

Résumé : La coupe à blanc a un impact esthétique important et modifie de façon significative les attributs de l'écosystème à de multiples échelles spatiales. Les changements abiotiques connus incluent l'augmentation des variations microclimatiques, les changements dans le bilan hydrique régional et la modification des patrons hydrologiques qui influencent les processus d'érosion. Les changements biotiques incluent l'augmentation de la richesse en espèces immédiatement après une coupe à blanc à cause des changements dans la composition en espèces qui résultent de la modification de l'abondance de certaines espèces et de la colonisation par les espèces d'habitats ouverts ou adaptées aux perturbations. Étant donné les changements écologiques importants causés par la coupe à blanc et la perception négative de ce type de coupe dans le public, il est surprenant de constater que peu d'études ont examiné si la réduction de la superficie coupée pouvait constituer une stratégie viable pour atténuer les changements écologiques dans chacune des coupes à blanc. Les études sur la dimension des coupes à blanc réalisées jusqu'à maintenant excèdent rarement une superficie maximale de 10 ha et les communautés biotiques mesurées ont des réactions mixtes à l'augmentation de la dimension de la coupe à blanc quant à la richesse en espèces et aux autres attributs de la biodiversité. Certaines réactions écologiques qui suivent la récolte ne sont pas linéaires relativement à la surface récoltée et laissent penser qu'il pourrait exister des seuils au-delà desquels les impacts de la coupe à blanc augmentent de façon disproportionnée par rapport à sa dimension. Les auteurs discutent des modèles conceptuels de seuil écologique potentiel dans les impacts de la coupe à blanc, étant donné le besoin de tests empiriques rigoureux pour s'assurer que les directives concernant les coupes en forêt reposent sur des bases solides.

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Introduction

As natural ecosystems are becoming increasingly degraded in many parts of the world, conservation of terrestrial biodiversity must increasingly look to production landscapes to achieve conservation goals (Knight 1999; Norton and Miller

2000; Novacek and Cleland 2001; Ewers and Didham 2006). Managed natural or planted forests represent one type of production landscape that makes a significant contribution to biodiversity at both local and regional scales (Spellerberg and Sawyer 1995; Chey et al. 1997; Norton 1998; Moore and Allen 1999; Brockerhoff et al. 2001; Hartley 2002).

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Plantations are known to provide alternative habitat for native species, improve connectivity between old-growth remnants, and buffer natural forests from edge effects, particularly in heavily modified landscapes where there is little unmodified forest habitat left. These biodiversity benefits remained largely unpublicized, whilst forest management practices often face heavy public criticism.

Environmental issues associated with forestry are controversial, particularly the extensive even-aged monocultural plantations (especially of exotic tree species) and the large-scale clear-fell harvesting that is typical of plantations and of many managed natural forests. It is indisputable that clear-felling results in substantial immediate on-site changes to the community structure and functional attributes of terrestrial ecosystems (Niemela et al. 1993; De Grandpre et al. 2000; Wardell-Johnson and Williams 2000; Roberts and Zhu 2002), their aquatic components (Rishel et al. 1982; Rowe and Taylor 1994; Stott and Marks 2000; Bubb and Croton 2002), and the aesthetic appeal of the landscape (McGee 1970; Hansis 1995). However, it is the combination of ecological change and the deep-seated underlying social values (which are difficult to influence and vary spatially) through which people interpret the visual changes associated with forest harvesting that modulates the acceptability of such practices (McCool et al. 1986; Bliss 2000).

Condemnation of clear-fell harvesting, especially by environmental nongovernment organisations, has been a significant driving force in forest policy (Schindler et al. 1993; Potton 1994; Rosoman 1994; Ribe 1999; Wilson and Wilson 2001). The acceptability of large-scale high-impact clear-fell harvesting is now reduced and in some countries restricted by voluntary mechanisms (industry-led agreements, such as the New Zealand Forest Accord (1991) and forest certification schemes, such as Forest Stewardship Council certification) or by legislation (e.g., the *Forest Regeneration and Clearcutting Standards* (Maine Forest Service 1999)). These restrictions are partially responsible for the increased implementation of alternative silvicultural systems over the last 20 years, including shelterwood harvesting, green-tree retention methods, and patch cuts. Numerous trials have assessed some of the impacts of these alternative harvesting techniques, and these have often included comparisons with clear-felling (e.g., Schowalter 1995; North et al. 1996; Volin and Buongiorno 1996; Franklin et al. 1997; Prescott 1997; Beese and Arnott 1999; Beese and Bryant 1999; Bohonak 1999; Perry et al. 1999; Bartman et al. 2001; Duguay et al. 2001; Moorman and Guynn 2001; Huggard and Vyse 2002; Koivula 2002b; Knapp et al. 2003). However, as Koivula (2002a) and Spence (2001) point out, the full ecological consequences and long-term ecological sustainability of these alternative strategies are still not fully understood.

Given that clear-fell harvesting has met with such strong opposition, it is surprising that few studies have investigated whether a reduction in the harvest area of individual clear-fells might be a viable strategy to mitigate ecological impacts. After all, some forest policies around the world restrict clear-felling by prescribing maximum size cuts. One of the assumptions underlying these policies is that there is a threshold size above which ecological change occurs at a rate that is socially unacceptable. The concept of ecological thresholds has been used in habitat fragmentation studies for some

years (Andren 1994) and more recently in ecological restoration (Hobbs and Norton 1996); in recent years the concept has found favour with land managers and territorial authorities (Huggett 2005). However, empirical evidence on which to base such policies is limited and individual fragmentation studies are often contradictory (Lindenmayer and Luck 2005). Empirical testing of forest harvest size thresholds has not yet been considered. What limited work that has been conducted on clear-fell size effects, at least at small spatial scales, was summarized by Bradshaw (1992), while a more extensive study in British Columbia is still in progress (Vyse 1999). In many ways it appears that the combined pressure of environmental nongovernment organisations and public opinion have circumvented research on the issue of ecological thresholds in clear-fell harvest size impacts, with most studies focusing on evaluating alternative silvicultural systems instead.

In this paper we begin by providing a brief overview of the on-site ecological changes induced by clear-felling in the context of plantations (including those of exotic species) and managed indigenous forests. We then review the few available studies on how clear-fell harvest size influences such ecological changes. This information is then combined to evaluate the possibility of a harvest size threshold at which ecological change occurs at a rate disproportionate to the change in harvest area. Different potential forms of this relationship are discussed in the context of recent ecological threshold studies in related disciplines of landscape ecology, with suggestions for designing empirical studies to test for threshold effects. The overall goal of this paper is to provide an increased understanding of the ecological consequences of harvest size in relation to large-scale clear-felling.

Impacts of clear-felling

Abiotic

The forest microclimate is strongly influenced by changes in overstorey canopy structure and is thus temporally and spatially variable (Chen et al. 1999). Harvesting practices such as clear-felling alter canopy structure and hence have an impact on the microclimate of forest stands (Chen et al. 1999; Burton 2002). Temperature, relative humidity, wind speed, and solar radiation are significantly more variable (both spatially and temporally) in clear-felled areas than in intact forest because of the removal of the buffering effect of the forest canopy (Chen et al. 1999; Zheng et al. 2000; Burton 2002; Spittlehouse et al. 2004) (Table 1). Steep edge-effect gradients can occur between stands with different microclimates (Chen et al. 1999).

Recently, conservation biologists have given considerable attention to the impacts of edge effects on indigenous biodiversity (Murcia 1995; Didham et al. 1998; Laurance 2000; Ries et al. 2004; Ewers and Didham 2006), including the impacts on managed forests, particularly at their boundaries with other habitats, for example, grassland (Magura et al. 2001). However, forest types differ in their vegetation structure and rates of secondary succession following disturbance (Brockerhoff et al. 2003). As a result the persistence and penetration of microclimatic edge effects, which are dependent on the rates of vegetative regrowth, will vary with biogeographic region, for example, tropical forest edges rap-

Table 1. Summary of the known short-term ecological changes in species abundance, richness, and composition of different taxonomic groups and abiotic changes induced by clear-fell harvesting.

Abiotic factor or taxon	Impact	Important points	Reference
Abiotic factor			
Microclimate	-/+	Temperature, relative humidity, light, and windspeed become more variable postharvest	Chen et al. 1995; Zheng et al. 2000; Spittlehouse et al. 2004
Snowmelt, accumulation, and ablation	-/+	Increased snow in harvested areas and increased rates of snow melt postharvest compared to intact forest	Hudson 2000; Murray and Buttle 2003
Stream flows and hydrology	+	Stream flows increase postharvest	Bosch and Hewlett 1982; Bubb and Croton 2002
Stream temperature	-/+	Stream temperature generally increases; however, extent dependent on riparian buffer management strategies	Rishel et al. 1982; Rowe and Taylor 1994; Stott and Marks 2000; Young 2000
Soil loss due to erosion	+	Soil loss and stream sedimentation can increase postharvest	France 1997
Species abundance			
Bats	-/+	Species specific, dependent on body size and foraging strategy	Patriquin and Barclay 2003
Spiders	-/+	Species specific, most impact on web-builders	Coyle 1981
Salamanders	-	Harvest impacts just as severe in leave tree, group selection, or shelterwood	Knapp et al. 2003
Birds	-	Abundance still reduced for one-third of all species after 14 years	Williams et al. 2001
Nematodes	-	Clear-fell impact as severe as in shelterwood treatments	Panesar et al. 2000
Stream macroinvertebrates	-	Returned to normal after spring rain, affected by increased sediment load associated with harvesting	Growns and Davis 1994
Plants	-	Decreased herbaceous layer cover	Gilliam 2002
Species richness			
Carabidae	+	Increased open-habitat species in many cases led to increased overall species richness	Atlegrim et al. 1997; Beaudry et al. 1997; Heliola et al. 2001
Stream macroinvertebrates	-	Returned to normal after spring rain, affected by increased sediment load associated with harvesting; dependent on depth in stream sediment	Growns and Davis 1994; Trayler and Davis 1998
Lucanidae	+	Some species may not survive in long term in clear-fell areas and require old-growth conditions	Michaels and Bornemissza 1999
Birds	+	Some species did decline in abundance	Baker and Lacki 1997
Species composition			
Spiders	-/+	Different response from visual pursuit, microweb, and trap-door spiders	McIver et al. 1992
Ectomycorrhizae	-/+	Driven by changes to soil biology and chemistry	Hagerman et al. 1999; Jones et al. 2003
Beetles	-/+	Changes between forest generalist and open-habitat species	Niemela et al. 1993
Plants	-/+	Changes in abundance of shade-tolerant and open-habitat species	De Grandpre et al. 2000
Small mammals	-/+	Change in fauna in open-habitat areas	Hansson 1994

Note: Change is recorded as positive (+), negative (-), or variable (-/+).

idly produce an edge understorey that buffers the microclimate within the remaining forest (Didham and Lawton 1999).

Land-use change and forest harvesting have considerable impacts on rates of snow accumulation and melt (Hudson 2000; Murray and Buttle 2003) and thus on the local water balance. In high-latitude forests, snow melt is a significant part of the annual water balance. Snow accumulation is often higher in harvest areas than in intact forest, especially in small- to medium-sized harvest areas and to a lesser extent in large clearings (as snow is blown away from large clear-fells into adjacent forest) (Hudson 2000; Murray and Buttle

2003) (Table 1). However, the difference between clearfell and forest snow accumulation is greater in coniferous than in hardwood forests because the more open hardwood canopy allows increased snow penetration (Murray and Buttle 2003). Snowmelt is greater in clear-fell areas than in forests under radiant melt conditions (Adams et al. 1998; Huggard and Vyse 2002). However, the difference in snow ablation between forest and clearfells, caused by rain falling on snow, is dependent on canopy snow loading (Beaudry et al. 1997 cited in Hudson 2000). Irrespective of clear-fell harvesting or canopy cover, the spatial variation in snowmelt rates is

most strongly influenced by geographical aspect, that is, north- versus south-facing slopes (Murray and Buttle 2003).

In warmer climates the influence of tall vegetation (e.g., trees) on dry and wet leaf evaporation will be more important in determining catchment water yield (see recent review by Davies and Fahey (2005)). Reduction in tall vegetation within catchments has been shown to increase stream flow (Bosch and Hewlett 1982) and create a temporary rise in stream temperature due to an increase in solar radiation on the water surface (Rishel et al. 1982; Rowe and Taylor 1994; Stott and Marks 2000; Kiffney et al. 2003), unless appropriate riparian management is undertaken (Young 2000). However, preliminary data suggest that flow rates return to preharvest levels as regeneration proceeds (Bubb and Croton 2002) (Table 1). There are also significant regional differences in the change in water yield in response to afforestation and forest harvesting (Rowe 2003). In addition to altered evaporation, the decrease in litter and coarse woody debris (especially from site preparation, e.g., windrowing) can reduce rainfall infiltration rates, further increasing overland flow (France 1997; Costantini and Loch 2002).

Increased overland flow increases soil erosion; however, clear-felling is not necessarily as damaging in this regard as other harvesting techniques. For example, group selection was shown by Hood et al. (2002) to erode 25.1 t/ha more soil per 100-year rotation than did clear-fell harvesting. This is probably induced by the increase in temporary roads required for group-selection harvesting. Sedimentation rates in stream channels can increase as a result of this enhanced erosion (France 1997) and affect surface communities as well as deeper streambed fauna (Trayler and Davis 1998). A buffer strip along a waterway is the management response designed to prevent increased sedimentation (Young 2000); however, insufficient testing has been done at a catchment scale of commonly used buffer strip widths, some of which may prove to be inadequate (Kiffney et al. 2003).

Biotic

The change in composition of biotic communities as a result of clear-fell harvesting has been well studied. Despite this, there is a paucity of information on some groups, particularly invertebrates, herbaceous vegetation, and fungal communities, all of which provide important ecosystem services. Table 1 gives an overview of some research findings with respect to the impact of clear-felling on species richness, abundance, and composition of different taxa.

Plants

Harvesting releases resources otherwise monopolized by the mature canopy species, allowing opportunities for surviving understorey plants and new colonizers originating from the soil seed bank and seed rain (Burton 2002). As a result of rapid colonization by open-habitat specialists, plant species richness is usually greatest in the first few years following clear-felling (Freedman et al. 1994; De Grandpre et al. 2000; Burton 2002; Roberts and Zhu 2002) (Table 1). However, in many countries the presence of large numbers of exotic invasive species may significantly alter these regeneration patterns. For example, in New Zealand's exotic plantation forests the dominant colonizing grasses, herbs, and shrubs following clear-felling are adventive, although

some indigenous species present in the understorey prior to felling commonly resprout (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003).

Invertebrates

Most studies of change in invertebrate community assemblages post-clear-felling have used single taxonomic groups, often ground beetles in the family Carabidae (Coleoptera). Unfortunately, these studies are often undertaken with little or no robust statistical justification as to the suitability of the chosen indicator species, citing abundance, sensitivity to environmental change, taxonomic and ecological knowledge, and ease of carabid sampling as justification for their use (Koivula 2002b; Magura 2002; Brouat et al. 2004).

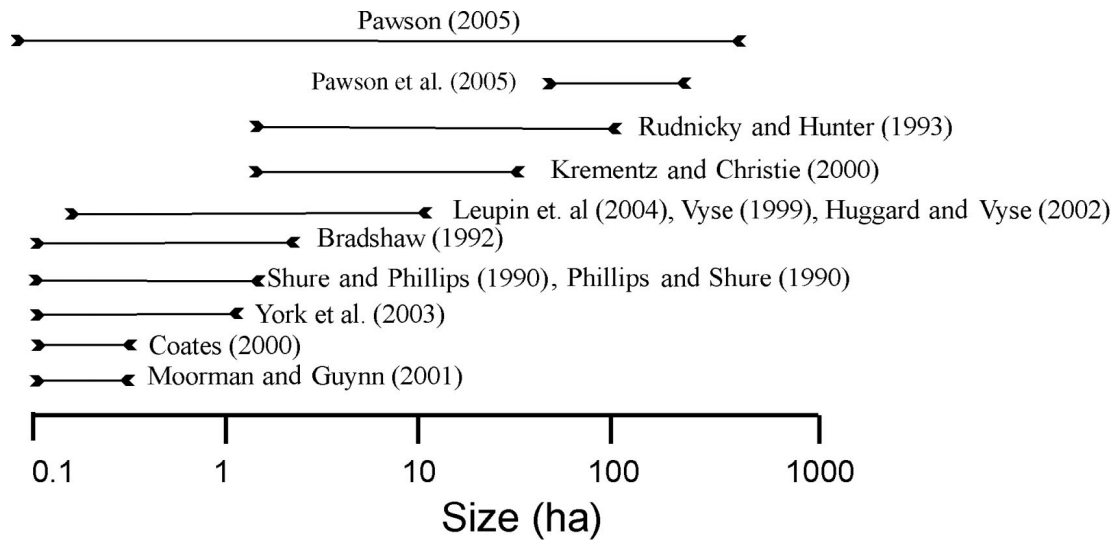
Previous studies have shown that clear-felling results in the loss of some insect species, but just like plant communities there is often an increase in species richness associated with colonization by open-habitat specialists, for example, beetles (Lenski 1982; Niemela et al. 1993; Butterfield et al. 1995; Spence et al. 1996; Beaudry et al. 1997; Niemela 1997; Fahy and Gormally 1998; Ings and Hartley 1999; Heliola et al. 2001) and ground-hunting spiders (Coyle 1981; McIver et al. 1992) (Table 1). The influx of open-habitat specialists is a transitory phenomenon, but in some Canadian and Finnish managed indigenous forests, species richness does not peak until approximately 10 years after harvest (Niemela 1997), and in some cases open-habitat species are still present after 27 years of stand regeneration (Spence et al. 1996). As such, the ecological impacts of these open-habitat species on forest specialist species may be of significance for very long time periods, although this has not been tested.

Birds

Forest canopy structure determines the availability of nesting and foraging resources for birds (Williams et al. 2001) and therefore influences the species richness and composition of resident bird communities (Clout and Gaze 1984; Wardell-Johnson and Williams 2000). Clear-fell harvesting typically creates large, even-aged, homogeneous stands with reduced resource diversity, which has been shown to limit bird abundance and species richness (Beese and Bryant 1999; Moore and Allen 1999; King and DeGraaf 2000; Wardell-Johnson and Williams 2000; Williams et al. 2001). However, it is the concomitant change in species composition (Clout and Gaze 1984; Hansson 1994) that is probably of greater importance. Large even-aged forests tend to favour open-habitat and generalist bird species postharvest. As such, it is unsurprising that recent clearfells and young forests are dominated by early-successional transient species and, in some countries, mainly exotic species (Clout and Gaze 1984; Hansson 1994; Wardell-Johnson and Williams 2000), while older regenerating and mature forests have higher proportions of forest generalist and old-growth bird species (Clout and Gaze 1984; Wardell-Johnson and Williams 2000).

Across all taxonomic groups there is concern that old-growth species in general may be lost from short-rotation clear-fell harvest systems because of a lack of suitable habitat, poor dispersal abilities, and (or) a lack of source populations (Clout 1984; Clout and Gaze 1984; Niemela et al. 1993; Spence et al. 1996; Wardell-Johnson and Williams

Fig. 1. Spatial scale of studies that focus on the ecological changes resulting from different clear-fell harvest sizes. Note that the scale is logarithmic.



2000). However, conflicting evidence does exist, such as forest specialist carabid beetles that have colonized newly established plantation forests in the UK, despite a lack of obvious source populations in the immediate vicinity (Jukes et al. 2001). Similarly, a rare carabid beetle *Holcaspis brevicula* is only known from an isolated exotic pine plantation on the Canterbury Plains (New Zealand), an area retaining less than 1% of the original native forest and scrub communities (Brockerhoff et al. 2005). This indicates that some forest-specialist and rare species have sufficient dispersal capabilities and tolerance of disturbance to maintain populations in newly established, repeatedly clear-felled forests and apparently move between existing forest areas. Whether these species represent exceptions from a general trend needs further investigation, as dispersal abilities are a key attribute to overcoming impacts of larger clearfells.

Impacts of clear-fell harvest size

Few published studies exist on the functional relationship between clear-fell harvest size and degree of ecological change at spatial scales relevant to current forestry practices. As such, it is difficult to determine whether there is a threshold clear-fell size beyond which there is a disproportionate increase in ecological change with increasing harvest area. Indeed, few studies have even sampled different-sized harvest areas, and most of these have focussed on gap-regeneration ecology at sizes of less than 1 ha (Fig. 1). These studies concentrated largely on tree regeneration rates, but in some cases measured biodiversity attributes, including bird diversity (Moorman and Guynn 2001). However, there continues to be a lack of comparative sampling or experimentation over larger harvest areas, making it difficult to gauge the nature of the relationship between harvest area and ecological impact.

Plants

Phillips and Shure (1990) reported significantly greater vegetative regrowth in 2–10 ha clearfells (1 year after clear-felling) than in smaller 0.016 ha clearfells in the southern Appalachians. In contrast, Moorman and Guynn (2001) failed

to find similar vegetative trends in canopy gaps of the same size in bottomland hardwood forests of the Upper Coastal Plain of South Carolina. In Phillips and Shure's (1990) case, the increase in vegetative growth was a reflection of more prolific stump sprouting in large clear-felled areas and was attributed mainly to increased solar radiation induced by larger scale canopy removal. Coates (2000) in a study of commercial tree species showed that plant growth rates increased with harvest area up to 0.2 ha, yet growth rates increased little between 0.2 and 0.5 ha. This is probably attributable to edge effects limiting solar radiation in forest gaps up to one tree height in radius (Spittlehouse et al. 2004). In contrast, York et al. (2003) extended the spatial scale of the study up to 1 ha gaps and found that growth rates were still increasing at this maximum gap size. The lack of consensus between studies illustrates that further research is required, particularly at larger spatial scales.

Indirect evidence of clear-fell size impacts suggests that even relatively large clearfells (100–120 ha) in plantation forests in New Zealand are recolonized by some indigenous forest plant species during a single rotation (ca. 27 years) (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003). However, the ability to colonize such large clearfells will be influenced by the relative dispersal abilities of different species, characteristics of the available seed bank, and the proximity and size of source populations. The combination of dispersal ability and rotation length has significant implications for the recolonization of clearfells of different sizes and requires further investigation.

Birds

Early-successional bird species are currently in decline throughout parts of the United States (Krementz and Christie 2000). This may in part be a function of their populations being unnaturally high after centuries of habitat loss that created early-successional habitat which is now being allowed to regenerate. Nonetheless, clearfells provide important, recently disturbed habitat for these species, and manipulation of harvest practices has been suggested as a way of managing them in modified landscapes. Krementz and Christie (2000)

found no decrease in reproductive effort, relative abundance, or species richness of early-successional bird species with increasing harvest area (2–57 ha) in a *Pinus palustris* forest in South Carolina. However, this is not surprising, as early-successional species might be expected to benefit from such harvesting practices. Other studies of entire bird communities have yet to show consistent changes in species richness per plot over different clear-fell sizes. For example, Leupin et al. (2004) observed no consistent changes in species abundances following clear-felling in smaller harvest areas (<0.01–10 ha).

Moorman and Guynn (2001) showed an increase in species richness with increasing harvest area from 0.06 to 0.5 ha, and Rudnický and Hunter (1993) found similar results at slightly larger spatial scales up to 20 ha. At even larger spatial scales (48–132 and 218–240 ha), Spurr and Coleman (2002) found no difference in the species richness of birds as a result of clear-fell harvest size.

Overall, it appears from the available evidence that clear-fell harvest size has few (detectable) negative effects on the species richness of bird communities over the range of clear-fell sizes and ages tested. Even Rudnický and Hunter (1993), who found the most compelling evidence for an effect of harvest area, recognised that clear-fell size was not the most important factor for most bird species using managed forests. Clear-fell size may have profound impacts on subsequent recolonization by forest species, as larger clearfells may impose greater constraints on individuals displaced by harvesting; however, this has yet to be tested.

Insects

Both species richness and relative abundances of arthropods were similar across all clear-fell sizes (0.016–10 ha) at the beginning of the season in Shure and Phillips' (1991) study in the southern Appalachian Mountains. Later, during the growing season, abundance and species richness in the small and large clear-felled areas approximately doubled, but remained unchanged in mid-sized (0.08–0.4 ha) clearings. High arthropod diversity in the small and large openings was attributed to a confounding variable, vegetation cover; greater vegetation cover supplied food and protection from the adverse microclimatic changes associated with clear-felling (Shure and Phillips 1991). Most importantly, different groups of arthropods responded differently to variation in clear-fell size in two independent studies (Shure and Phillips 1991; Huggard and Vyse 2002). Millipedes, spiders, beetles, and ice crawlers (Grylloblattodea) decreased in abundance with clear-fell size, whilst slugs and Homoptera tended to increase in abundance with increasing clear-fell size (Shure and Phillips 1991; Huggard and Vyse 2002). Meanwhile, some spiders and ants exhibited nonlinear responses and had decreased abundance in mid-sized clear-fell areas (Shure and Phillips 1991).

Reference points for testing clear-fell harvest impacts

The majority of the aforementioned studies of ecological change with respect to clear-fell harvest size have used comparisons among clearfells, rather than comparisons against a fixed reference point, such as unharvested interior forest.

However, a few studies have made direct comparisons, including Leupin et al. (2004), who compared bird abundance in different harvest sizes with a control forest and individual-tree selection (30% tree removal) and found that Golden-Crown Ringlet (*Regulus satrapa*) abundance decreased significantly in all harvest areas compared to control stands, whereas both individual-tree selection systems and 10 ha clear-fell harvest treatments had lower abundance than did smaller 1 ha clearfells. In a comparison between different clear-fell sizes and uncut adjacent stands of *Pinus radiata*, Pawson et al. (2005) showed that *Pycnomerus sophorae* (Coleoptera: Zopheridae) had greater abundance in small 0.05 ha clearfells than in uncut adjacent forest, but lower abundance than in the reference stand in larger clear-fell areas. The use of reference points as a base line for comparison is critical to the interpretation of harvest impacts.

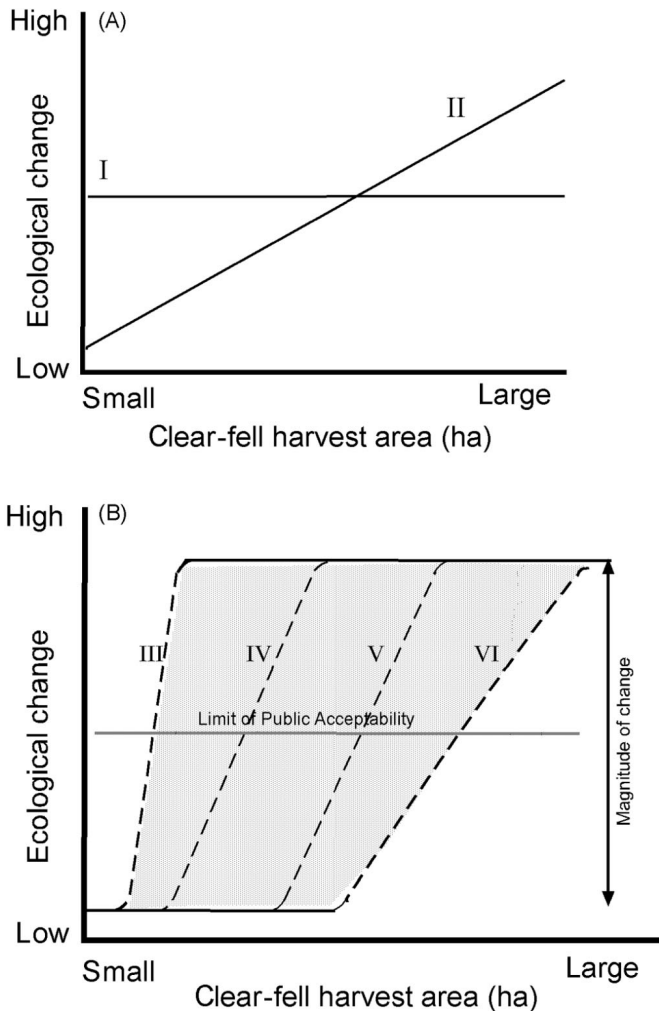
Perhaps because of the perception that clear-fell harvest sizes might have to be very small to remain essentially unchanged from the ecological conditions in uncut forests, there has been a growing interest in legacy management, for example, variable-retention harvest as a method for reducing the severity of ecological change of even-aged forest management (Mitchell and Beese 2002). However, it is only recently that studies such as those of Mazurek and Zielinski (2004) and Bebbler et al. (2005) have provided direct evidence for the value of legacy management as a method of improving biodiversity conservation in even-aged harvesting systems. In this context, a comparison of clear-fell harvest areas to uncut forest, with and without legacy management, would be particularly instructive. For example, does legacy management protect conservation values across the entire spectrum of clear-fell sizes or does the importance of legacy management decrease with increasing harvest area? Most importantly, in all such comparative studies between clear-felling and uncut forest, or alternative harvesting systems, there is a need to sample across a wide range of taxa and ecological processes to ensure that ecosystem-level responses are measured, rather than individual taxon responses that may not be representative of the majority of species.

Other potentially important reference points to consider are natural-disturbance clearing in forests, given intense interest in the hypothesis that clear-fell harvest areas may mimic natural disturbance processes such as windthrows or catastrophic wildfires. The ecological similarity of clearfells and natural disturbances, including the effects of postharvest treatments, has been the subject of many studies (Gluck and Rempel 1996; Quine et al. 1999; Carignan et al. 2000; Lindenmayer and McCarthy 2002; Baker et al. 2004; Simon and Schwab 2005) and the issue remains contentious. As part of this debate consideration should be given to the fact that any similarity between clear-fell harvesting and the results of natural disturbance processes may change with harvest area, a point yet to be studied in detail.

The search for thresholds

We consider that the key focus of future research, and the concept of greatest interest to land managers, is the potential existence of a threshold clear-fell size, beyond which induced ecological change increases disproportionately to the linear increase in harvest area. The notion of ecological

Fig. 2. (A) Null hypothesis of no change (curve I) or a linear change (curve II) in ecological impacts with increasing harvest area. (B) Hypothetical scenarios for threshold ecological change across different clear-fell sizes (curves III–VI). Ecological change might occur sharply at a defined point or be spread over wider clear-fell sizes. The magnitude and rate of change (slope of line) are likely to vary depending on the response variable studied. As such, there may not be a single identifiable threshold point, but rather a threshold zone might be likely to occur (denoted with shading).



thresholds or discontinuities in response is not new (Muradian 2001; Huggett 2005), but it is only relatively recently that there has been a major focus on the theoretical and empirical importance of ecological thresholds. For example, in the extensive habitat fragmentation literature there is accumulating evidence of ecological thresholds in remaining habitat cover, below which there is a nonlinear decrease in population persistence in habitat fragments (Andren 1994; Fahrig 2001). However, recent empirical studies highlight inconsistencies in the location (or existence) of ecological thresholds across species and sites (Drinnan 2005; Lindenmayer et al. 2005; Radford et al. 2005), and Muradian (2001) and Huggett (2005) raise caution about the limited predictive abilities of such empirical threshold estimates. Despite this, the concept of ecological thresholds has found great utility with territo-

rial authorities who manage land for conservation purposes, particularly in Australia (Huggett 2005).

So what is the range of likely responses of ecological communities to clear-fell harvesting (Fig. 2)?

- Harvest impacts may follow the null hypothesis of no change in biodiversity and ecosystem function after harvesting (curve I in Fig. 2A), although this is unlikely for the majority of response variables given known changes in abiotic and biotic factors discussed earlier.
- Responses may be linear in that ecological change is proportional to harvest size (curve II in Fig. 2A), that is, there is no critical breakpoint or threshold in the system.
- A third possibility is that there is a threshold effect, in which ecological change increases are disproportionate to the increase in harvest area, although there are several alternative scenarios for the location and shape of the threshold effect across harvest areas (Fig. 2B). Ecological change may occur rapidly at very small harvest sizes and then plateau with little change beyond this small critical size (curve III in Fig. 2B).
- Alternatively, threshold points may occur at larger clear-fell sizes and the transition between low and high ecological impacts may be more gradual (curves IV–VI in Fig. 2B).

The species responses discussed in previous sections, for example, lack of change in bird species richness in clearfells over 20 ha (Rudnicki and Hunter 1993), suggest that nonlinear responses to clear-fell harvesting do exist in at least some circumstances. Given these nonlinear responses, at what harvest size might threshold points occur and where should research effort be concentrated to quantify this threshold size? The magnitude of the change postharvest will vary depending on the response variable measured, as well as broad-scale biogeographic factors such as forest type and fine-scale factors such as aspect and slope (Fig. 2). Consequently, there is most likely to be a threshold zone of ecological transition (indicated by the shaded area in Fig. 2B), and exact thresholds will vary spatially and temporally depending on response variables (e.g., species abundance, community composition, and so on) and stand-specific factors.

Definitions of the harvest area that defines the term “clearfell” have focussed on changes in microclimate. Given that microclimate is a key variable that determines species distributions and community composition and influences biological processes (Krebs 2001), the change between a forest microclimate and a clear-fell or open-habitat microclimate seems a logical starting point to assess ecological thresholds in the response of biodiversity to clear-fell harvesting. Most definitions of clearfells have assumed an area with a radius greater than one to two tree heights (Bradshaw 1992). Recent research into microclimatic changes induced by clear-felling at Sicamous Creek, British Columbia, supports this, showing that the greatest rate of change occurred within one tree height of the forest edge (Spittlehouse et al. 2004). Therefore, clear-fell areas above or below one to two tree heights in radius become a logical starting point to test for clear-fell thresholds and changes in forest biodiversity. This size will vary depending on forest type, topography, and local climate.

In addition to potential ecological thresholds resulting from clear-felling there is a strong social element of public acceptability to take into consideration. It is likely that there

are limits to public acceptability of clear-fell harvest impacts that may differ greatly from the amount of ecological change observed (Fig. 2B). As yet there is no empirical evidence to define where (or if) these ecological thresholds in clear-fell size exist, and as such we are not in a position to reconcile any potential differences between forest policy and public perceptions. However, a mismatch between the ecological threshold and public acceptability creates potential conflict, especially if the ecological threshold is higher than the limits of public acceptance.

Discussion and conclusions

Disturbances of the magnitude produced by clear-fell harvesting will cause significant changes in abiotic factors such as microclimate and hydrology, which in turn affect local biotic communities. In the past, clear-felling has been promoted as a mimic of natural processes, such as wild fire and windthrow, although in recent years such comparisons have been questioned. Clear-felling may be an adequate mimic of disturbance in some forest systems (Seymour and Hunter 1999), but the extent of similarities can in some cases be quite superficial, with forestry providing a poor substitute (Spence 2001; Pedlar et al. 2002).

Clear-fell harvest size has been reduced or replaced by alternative silvicultural systems in recent years, largely because of public pressure, but in some cases also for specific ecological reasons (e.g., concern over population decline in the Spotted Owl (*Strix occidentalis*); Noon and McKelvey 1996). It appears, generally speaking, as if there has been an a priori assumption that large clearfells are "bad", yet from the available research there is conflicting empirical support for this generalization (Phillips and Shure 1990; Shure and Phillips 1991; Rudnicki and Hunter 1993; Huggard and Vyse 2002; Spurr and Coleman 2002; Leupin et al. 2004).

Public acceptability is partially driven by science and to a large degree by social values. Unfortunately, the data for critically assessing ecological change as a function of clear-fell size is lacking. As such, forest managers lack crucial information to facilitate consultation with the public over their management practices. Further complications will occur when comparing managed native forests with plantations formed by the reforestation of previously agricultural land. Public perception of plantations is different from that of managed native or old-growth forests, and these differing attitudes will affect the acceptability of clear-felling depending on the forest context. In addition, the actual impact of clear-felling may also be context dependent, because the process of afforestation to create plantations may select for species with good dispersal abilities and generalist habitat requirements that are better suited to cope with clear-fell harvesting methods. As a result, many species in recently reforested agricultural landscapes may be less affected by large-sized cuts than those present in managed indigenous forests.

Large-scale clear-felling may be the most cost-effective form of harvesting currently available, especially for low-value timber species. However, considerable research is still required to determine the ecological change induced by different-sized clear-fell harvest areas across the spectrum of currently managed forests, including different forest types

(managed indigenous, exotic, and native plantations), as well as a range of biogeographic zones. This research is important to identify possible thresholds where the severity of ecological damage changes dramatically. Previous work on microclimatic changes induced by clear-felling would indicate that a large amount of change occurs in forest gaps greater than one tree length in radius. As such, research should be targeted at assessing impacts from <1 to 10 ha to identify potential threshold points. However, comparisons with uncut forests and with larger clear-fell areas will also be necessary to confirm the shape and magnitude of the impact curve (Fig. 2) and to determine responses of other abiotic and biotic variables.

Threshold sizes, if they exist, can guide forest management, enabling the development of improved harvesting policies. However, potential thresholds of one to two tree lengths in radius will be significantly smaller than current forest harvesting practices in many countries. This will be a contentious issue that will need addressing in due course.

Research and policy design needs to be followed by a process of public education. The point needs to be made that not all forestry activities are bad for biodiversity (Pawson and Brockerhoff 2005), especially with respect to plantation forestry in areas that have otherwise lost the majority of native tree cover. In some instances, establishing plantations on marginal agricultural land can be beneficial for regional forest biodiversity. In such cases, silviculture can have positive conservation outcomes, but to ensure its sustainability and gain broad public acceptance, it must be based on sound science.

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