

Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning

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Summary

Single-species conservation and natural reserves seem insufficient for protecting biodiversity to scientists, and conventional forestry seems suspect in sustainability to much of the public. In northwestern USA, comparisons of natural and managed coniferous forests support the idea that both single-species conservation and conventional forestry are unlikely to be successful because biocomplexity is more important than individual habitat elements in maintaining the diversity of forest ecosystems and their capacity to produce useful goods and services. Experiments in inducing heterogeneity into forest canopies support the importance of biocomplexity to various biotic communities including soil organisms, vascular plants, fungi, birds, small mammals and vertebrate predators. Holistic management, however, requires a suite of techniques to direct developmental processes to useful trajectories.

Introduction

It is time to move beyond reserves into managing forests to conserve biodiversity (di Castri and Younes, 1990; Entwistle and Dunstone, 2000; Korpilahti and Kuuluvainen, 2002). World wide, people are demanding environmental and economic sustainability (Reid and Miller, 1989; Goodland, 1995; Folke *et al.*, 1996). Conservation of biodiversity is the fundamental guiding principle for ecologically sustainable forest management (Larsson and Danell, 2001; Lindenmayer and Franklin, 2002). Forestry in Europe has to demonstrate sustainability by providing wildlife habitat (Larson, 2001; Pommerening, 2002; Nordlind and

Ostlund, 2003). In northwestern USA, forests are expected to provide commodities; revenues for land owners, schools and roads; economic support to local communities; habitat for forest wildlife and plants; recreational and spiritual experiences; and clean air and water (Carey *et al.*, 1999b; Carey and Wilson, 2001). Timber management, however has simplified forest ecosystems (Franklin 1993a,b; Carey *et al.*, 1999a, b), enabled invasion by exotic species (Hobbs and Humphries 1995; Halpern *et al.*, 1999; Thysell and Carey 2001), imbalanced biotic communities (Aubry 2000; Carey, 2000b; Haveri and Carey, 2000; Wilson and Carey, 2000; Carey and Harrington 2001), reduced prey biomass for predator (Carey *et*

al., 1992) and produced poorly functioning food webs (Carey *et al.*, 1996, 1999a 2002; Colgan *et al.*, 1999). In the Pacific Northwest, natural forests and contemporary managed forests differ in structure, composition and function (Carey, 1995; Carey and Johnson, 1995; Carey *et al.*, 1999a; Carey and Harrington, 2001). In natural forests many ecosystem elements are patchily distributed. These elements include live trees from the preceding stand, large fallen trees, trees with cavities used for denning and nesting, berry bearing shrubs, shade-tolerant trees in the midstorey, forbs, mosses and fruiting bodies (truffles) of ectomycorrhizal fungi, among others. Groups of these elements may be correlated in their occurrences (e.g. due to topographic effects or canopy gap formation) and, thus, form distinct patches. Diverse patches, arrayed in fine scale, contribute to emergent properties, such as simultaneously high abundances of potentially competing species that do not occur together in high abundances in large, homogeneous patches. The scale of variation in arrangement that contributes to this synergy is about 0.1-0.5 ha or 80-100 m (Canham *et al.*, 1990; Carey *et al.*, 1999a). Biotic legacies from preceding forest, propagules from adjacent stands, forest structuring processes and development of spatial heterogeneity interact to produce both overall compositional diversity and patch diversity (habitat breadth) (Carey *et al.*, 1999a; Franklin *et al.*, 2000). In contrast, stand tending focused on timber production, particularly even-age management, purposefully reduces spatial heterogeneity and compositional diversity (Carey, 2000b; Carey and Harrington, 2001). Consequently, the response of species to changes in abundances of particular elements of their habitat varies from place to place in managed forests, in relation to the relative abundances of other ecosystem elements. The diversity and structure (biotic integrity) of vertebrate communities, however, varies consistently in response to complexity of vegetation structure and absence of various compositional elements because spatial heterogeneity and compositional diversity (biocomplexity) in plant and fungal communities is pre-requisite to pre-interactive niche diversification, animal community diversity and the ability of ecosystems to resist or recover from disturbance (ecosystem resilience) (Hutchinson, 1978; Tilman, 1996, 1999; Carey *et al.*, 1999a).

Forest management can promote biocomplexity (Carey *et al.*, 1999a, b). Retention of legacies of individual live trees, dead trees, coarse woody debris, or even patches of forest can be used with even-age or uneven-age management systems (Franklin *et al.*, 2000). Variable-retention harvest systems transcend traditional silvicultural conventions (Franklin *et al.*, 1997). Thinning influences all structuring processes, including decadence and development of spatial heterogeneity. Thinning with underplanting restores tree species diversity and accelerates canopy stratification and understorey development. Retaining decadent trees, wounding trees and inoculating trees with top-rot fungi promote decadence essential to ecosystem development (Franklin *et al.*, 1987; Carey *et al.*, 1999a).

In 1991, I began an experiment to test the efficacy of various techniques for ecological restoration (Carey *et al.*, 1999c). I used variable-density thinning (VDT) to induce heterogeneity into tree canopies (hereafter referred to as 'mosaics'), underplanting to restore lost tree species diversity and decadence management (including inoculations of top-rot fungi) for cavity trees to accelerate ecosystem development in stands with two common management histories - timber management with conventional thinning (hereafter 'timber') and passive forest management with retention of biological legacies (hereafter 'legacy'). I measured responses of soil organisms, plants, birds and mammals for 5 years after VDT; it is too early to evaluate underplanting and fungal inoculations. Thus, I present here a short synthesis of published results on the efficacy of VDT in restoring biocomplexity to even-aged, temperate coniferous monocultures.

Methods

Study sites

My study is south-east of Olympia, Washington, USA, 46° 55' 42" to 46° 59' 00" N and 122° 40' to 122° 42' W (Carey *et al.*, 1999c). Soils are coarse-textured gravelly sandy loams. Elevation is 120-165 m; relief is flat to rolling on glacial outwash plains. Annual precipitation is 800-900 mm with only 10-15 per cent during the summer. Vegetation is temperate coniferous forest - the

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)—ocean spray (*Holodiscus discolor* (Pursh.) Maxim.) association of the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone. The study includes 16 13-ha stands in four blocks in a randomized complete blocks design. Each stand is subdivided into 64 0.16-ha cells by an 8 X 8 grid with 40 m between grid points; a 40-m border surrounds the grid. The grid is the template for treatments and sampling.

Two timber blocks were clearcut in about 1927 and conventionally thinned twice to a final density of 225 ± 16 and 236 ± 22 trees ha^{-1} (~ 7 in between trees) >10 years prior to initiation of my study. Few ($<1 \text{ ha}^{-1}$) trees were retained from the preceding stand and dead trees were removed. Canopy trees were 54 ± 5 and 51 ± 5 cm in diameter at 1.5 m above ground; cover of coarse woody debris was 2-3 per cent; cover of understorey vascular plants was 89 ± 9 and 87 ± 6 per cent, dominated by salal (*Gaultheria shallon* Pursh), swordfern (*Polystichum munitum* (Kaulfuss) K. Presl.) and brackenfern (*Pteridium aquilinum* (L.) Kuhn.). Shade-tolerant conifers were rare.

Two legacy blocks were clearcut in about 1937, with 2.7 live trees ha^{-1} and 3.5 dead trees ha^{-1} retained from the preceding old growth. Woody debris included old decaying fallen trees (7-8 per cent cover), stumps of old trees (48 ha^{-1}) and abundant (3 per cent cover) small trees killed by suppression or root rot (*Phellinus weirii*). Understorey cover was patchy, averaging 34 ± 5 per cent in both blocks, dominated by salal. Canopy densities were 598 ± 33 and 641 ± 45 trees ha^{-1} and 35 ± 2 and 33 ± 4 cm in diameter at 1.5 m. Few shade-tolerant conifers were present.

Treatments

Treatments were randomly assigned to stands within blocks in 1993 and included controls (no treatment), VDT with underplanting, supplementary dens (and fungal inoculations) for northern flying squirrels (*Glaucomys sabrinus*) and VDT combined with the dens treatment. Here, I focus on inducing heterogeneity with VDT because it is too early to evaluate effects of underplanting and fungal inoculations. The dens

treatment had minor effects on flying squirrels (Carey, 2002). Thus, hereafter, I refer to controls (controls and dens treatments combined) and mosaics (VDT and VDT plus dens treatment combined), i.e. timber controls, legacy controls, timber mosaics and legacy mosaics.

Variable-density thinning creates canopy mosaics in second-growth stands to produce vegetative heterogeneity similar to that in old growth (Figure 1; Carey and Johnson, 1995; Carey *et al.*, 1999a). By removing subordinate and codominant trees, light, water, nutrients and space become available spatially in various amounts to other vegetation. Effects extend beyond the altered patches of canopy because of low sun angles. This fine-scale heterogeneity creates an even more diverse mosaic of environmental conditions and numerous patch types in the understorey (Canham *et al.*, 1990). Maps of natural mosaics revealed 0.1-0.5-ha patches with a 2 : 1 ratio of closed to open canopy (Carey *et al.*, 1999a).

I used relative density (RD) to determine how much to thin. The RD index to inter-tree competition in even-age evenly spaced stands is more accurately measured than canopy cover (Curtis, 1982). For Douglas-fir, RD ranges from 0 to a biological maximum of 14; excessive crown restriction occurs with $\text{RD} > 7$. Timber stands had $\text{RD} = 6.5$ and legacy stands had $\text{RD} = 7.2$. I randomly assigned RD values of 2, 4 and 6 to the 0.16-ha cells and $\text{RD} = 6$ for the 40-m buffer to achieve a 2 : 1 ratio of light (residual $\text{RD} > 4.75$) to heavy thinning ($\text{RD} < 4.75$) and mean residual RD of 4.8 in legacy mosaics and 4.7 in timber mosaics (Figure 1). Heavily thinned cells were planted with red alder (*Alnus rubra* Bong.), western white pine (*Pinus monticola* Dougl. ex D. Don), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and western red cedar (*Thuja plicata* Donn ex D. Don), chosen variously for resistance to root rot (*Phellinus weirii*), value in restoring lost biodiversity, tolerance of variation in soil moisture and shade tolerance. Shade-tolerant conifers are important because they exert more control over light regimes (and consequently spatial patterning) than the shade-intolerant Douglas-

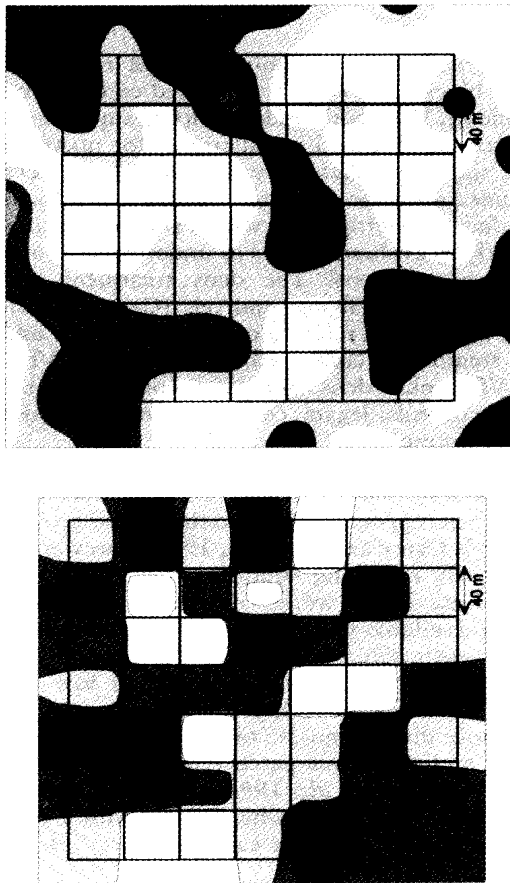


Figure 1. Recreating spatial heterogeneity characteristic of old forests in second-growth forest canopies with variable-density thinning. (A) Densities of trees >50 cm at 1.5 m above ground in a 280-year-old *Pseudotsuga menziesii* forest, shading (light to dark) represents densities from 3 to 45 trees ha^{-1} , based on 225 sampling points (from Carey *et al.*, 1999b). (B) Relative densities of *P. menziesii* >20 cm at 1.5 m following variable-density thinning of a 56-year-old second-growth stand; shading (light to dark) represents relative density classes of <math><3.25</math>, 3.25-4.75, 4.75-6.75 and >6.75 (from Carey *et al.*, 1999c).

fir with its tall, narrow crown.

Choice of response variables

The trophic pathway symbolic of Pacific Northwest ancient forests includes the northern spotted owl (*Strix occidentalis*), northern flying squirrel, ectomycorrhizal fungi and Douglas-fir (Carey, 2000a). The spotted owl is a species now threatened with extinction. The flying

squirrel is the primary prey of the owl. Truffles (hypogeous ectomycorrhizal fungal sporocarps) are the primary food of the squirrel. The squirrel disperses truffle spores and associated microorganisms (Li *et al.*, 1986) throughout the forest. Mycorrhizal fungi enhance the ability of Douglas-fir (and many other trees) to absorb water and nutrients from the soil and receive carbohydrates in return. The fungi move photosynthetic carbohydrates from trees to the mycorrhizosphere, a vast array of microbes, insects, nematodes, bacteria and other soil organisms.

Healthy Pacific Northwest forest soils are dominated by fungal mycelia and a shift from fungal domination to bacterial domination can signal impending loss of forest productivity (Ingham and Molina, 1991). Particularly sensitive to mechanical impacts are matt-forming fungi. Thus, ratios of total and active fungal mycelial biomass to total and active bacterial biomass, respectively, cover of fungal mycelial mats, and abundances of mycophagous, bacteriophagous and predatory nematodes provide measures of the biological impacts of forest management on forest soils (Ingham and Molina, 1991; Carey *et al.*, 1996; Colgan *et al.*, 1999). I was concerned with forest-floor function because it is the foundation for sustainability of forest ecosystems in the Pacific Northwest and elsewhere. Taxonomic diversity and biomass of truffles, on the other hand, are important in supporting squirrel populations; thus, I measured truffle diversity and abundance. But biological activity in the forest floor also depends on a variety of invertebrates that are important in nutrient cycling and as food for small mammals. Thus, I extended forest-floor function hierarchically to the integrity of the forest-floor small mammal community, which is particularly diverse in insectivores in Pacific Northwest forests (Carey and Johnson, 1995; Carey and Harrington, 2001).

Further above ground, the food web expands to include other raptors and mustelids; three species of squirrels; seeds, fruits and mushroom (epigeous fungal sporocarps); and various trees shrubs and

herbs. This expanded complex is more accurate in evaluating forest ecosystem function than any single species or a narrowly defined trophic pathway. This is true even within trophic levels; the changes in the structure (composition and relative abundances of species) of biotic communities in response to heterogeneity in canopies and to forest management generally is much more informative than changes in the abundances of single species (Carey, 1995; Carey and Johnson, 1995; Carey *et al.*, 1999a,b; Carey and Harrington, 2001). The spotted owl and other predators, however, respond to stands at the landscape scale (Carey *et al.*, 1992) and cannot be used to evaluate stand management at small scales. Thus, I measured abundances of three squirrels, the northern flying squirrel, the Douglas' squirrel (*Tamiasciurus douglasii*) and Townsend's chipmunk (*Tamias townsendii*), and compared them with the simultaneously high abundances of the three species in old-growth forest. While diets of the three species overlap, the flying squirrel is a truffle specialist, the Douglas' squirrel a conifer seed specialist and Townsend's chipmunk is a fruit generalist, feeding on conifers seeds, seeds and nuts of deciduous trees, berries of shrubs and truffles (but relegated to areas of high shrub cover). Not only does the combined biomass of these three species reflect production of fruits by plants and fungi, these three species also determine the carrying capacity of the forest ecosystem for a diverse assemblage of predators (owls, raptors and mustelids). Thus, their combined biomass is a measure of ecological productivity (Carey *et al.*, 1999b).

Because many animals respond to the structure and composition of the plant community (Carey *et al.* 1999a; Carey and Harrington, 2001), I measured abundance and diversity of vascular plants. Measures of spatial pattern are now underway (10 years post-treatment). Because mechanical disruption of soil and simplification of forests by timber management can promote invasion by exotics (Halpern *et al.*, 1999), I did record exotic species and tracked their tenure in the system.

Finally, resident birds play important roles in Pacific Northwest forest in regulating insect pest populations by insectivory, and in decadence processes by excavating cavities in trees

(Manuwal and Huff, 1987). These birds are particularly sensitive to the simplifying effects of timber management. Thus, I measured their diversity and abundance in winter.

Measurement of response variables

Significant results were compiled from published reports. Methods are described in the reports and briefly here. Understorey was measured in 240 nested nested 100-m² and 500-m² circular plots in July 1 and August before and 16 and 40 months after VDT (Carey *et al.* 1996; Thysell and Carey, 2000, 2001). Soil food web samples (fungal mycelia, bacteria and nematodes) were taken from a 100-plot subset of the vegetation plots (Carey *et al.*, 1996). Truffles were sampled every 6 weeks from April 1993 (immediately after VDT) to December 1995 with 160 4-m² plots for a total of 3680 plots of 14 720 m² (Colgan *et al.*, 1999; Carey *et al.*, 2002). Squirrels were captured in 2-week periods during spring and autumn, 1991 - 1998, with 2048 traps, half 1.5 m high in tree and half on the ground, for 135 000 trap nights and 8032 captures of 3183 individuals (Carey, 2000b, 2001). Smaller mammals were captured on 10 x 10 grids with 20-m spacing (4 ha) in the centre of the larger 8 x 8 grids. Two traps were placed at each point (3200 traps) and opened for 8 nights each summer for 5 years to get >70 000 trap nights and 9000 captures of 17 species, including eight species that compose the forest-floor mammal community (Wilson and Carey, 2000; Carey and Wilson, 2001). Timber and legacy controls were sampled in 1992, 1993 and 1994 to compare management histories; all 16 stands were sampled in 1996 and 1997 to determine responses to VDT. Winter birds were counted during four 10-min visits to nine stations >80 m apart in each stand (a total of 144 stations), 1996-1998, 1350 counts that recorded 7455 birds of 28 species (Haveri and Carey, 2000). Four conditions were compared: timber, legacy, timber mosaics and legacy mosaics.

Results

Soil food webs

Historical management appeared to influence the structure of soil food webs, but all stands seemed to retain fungi-dominated soils. Fungal to bacterial biomass ratios in legacy and timber stands were 123 : 1 versus 101 : 1 for total biomass and 2.4 : 1 versus 1.6 : 1 for active biomass, respectively. Total fungal biomass was 58 pg g⁻¹ of dry soil versus 21 Vg g⁻¹, respectively. Fungal mats covered 66 per cent of legacy controls compared with 25 per cent of timber controls. Mycophagous nematodes were 19-20 nematodes g⁻¹ of dry soil in both types. There were 16 bacteriophagous nematodes g⁻¹ in timber and 11 g⁻¹ in legacy controls. Predatory nematodes were most abundant in timber controls (2.5 g⁻¹ versus 2.0 g⁻¹ in legacy controls). Compared with controls, VDT had no effect on total biomass ratios, but increased the active biomass ratios to 2.6 : 1 in both timber mosaics and legacy mosaics. Total fungal biomass remained unchanged in timber mosaics but decreased to 44 pg g⁻¹ in legacy mosaics. Mycophagous nematodes decreased in timber mosaics but increased in legacy mosaics. Bacteriophagous nematodes and predatory nematodes increased with degree of disturbance within both mosaics.

Truffle biomass averaged 0.5 kg ha⁻¹ (ranging from 0 to 1.8 kg ha⁻¹ seasonally) in the timber and legacy controls. Of 28 species found in timber and legacy controls, 19 were in timber controls with seven only in timber controls. Of the 28 species, 21 were in legacy controls with nine only in legacy controls. *Rhizopogon* was the dominant genus, with a relative frequency of 40-47 per cent. *Gautieria* and *Leucogaster* were more frequent in legacy than in timber controls and *Melanogaster* and *Hysterangium* were more frequent in timber controls. Truffle production was reduced overall in mosaics (from an overall frequency of 18 per cent in control plots to 13 per cent in VDT plots) in the short term, with heavily thinned patches most reduced (to 10 per cent). Truffle diversity increased to 48 species in mosaics (versus the 28 species in controls) and productivity quickly recovered. *Gautieria* and *Hysterangium* decreased in abundance in mosaics, but *Melanogaster* increased in species diversity and biomass.

A total of 64 mushroom species was found before treatment, 37 (19 mycorrhizal) in legacy stands and 44 (15 mycorrhizal) in timber stands. Richness of ectomycorrhizal mushrooms was highest in legacy stands. After VDT, 108 mushroom species were found in legacy mosaics (versus 89 species in legacy controls) and 78 species were found in timber mosaics (versus 65 in timber controls).

Understorey plants

Legacy stands had 27-40 species of understorey plants compared with 49-87 species in the timber stands. Of 91 species in timber stands, 51 were not found in legacy stands and 18 were non-native species (1 tall shrub, 2 low shrubs, 13 herbs and 2 grasses). Of 47 species in legacy stands, four were not found in timber stands, including the old-growth associate Pacific yew (*Taxus brevifolia* Nutt.) and one was non-native. Community structure differed with management history, with timber stands dominated by aggressive clonal native shrubs and ferns. Timber stands had greater cover than legacy stands for total understorey (88 per cent versus 34 per cent), tall shrubs (12 per cent versus 5 per cent), salal (25 per cent versus 13 per cent), swordfern (16 per cent versus 3 per cent) and brackenfern (9 per cent versus 2 per cent). Compared with controls, mosaics initially had reduced understorey cover and increased importance of 20 native and 11 exotic species. Two native species decreased in importance. Three years later, understorey recovered, species richness increased by 150 per cent, only four exotic species persisted in importance and eight natives increased and seven natives decreased in importance. Underplanting was re-establishing root-rot resistant trees in root-rot pockets, increasing the resilience of the forest, and in other heavily thinned areas, increasing resistance to spread of root rot.

Small mammals

Timber stands had 1.5 times the numbers and 1.7 times the biomass of small mammals in legacy stands. Keen's mouse (*Peromyscus keeni*), a dominant species in natural forests, was rare in both forests. The creeping vole (*Microtus oregoni*)

was inordinately abundant in timber stands (3rd ranked) compared with legacy stands (7th ranked) and natural stands. The montane shrew (*Sorex monticolus*) was also inordinately abundant in thinned stands (2nd ranked). Neither management history produced communities typical of natural forests. After VDT, deer mice (*Peromyscus maniculatus*), creeping voles and vagrant shrews (*Sorex vagrans*) increased in abundance in mosaics. No species decreased in abundance.

Squirrels

Northern flying squirrels were twice as abundant in legacy as in timber stands (1.0 ha⁻¹ versus 0.5 ha⁻¹). Townsend's chipmunks were opposite (0.2 ha⁻¹ versus 0.8 ha⁻¹). Douglas' squirrels were low in abundance in both (0.1 ha⁻¹). Flying squirrels decreased in abundance in legacy mosaics immediately following VDT but recovered within 5 years. Chipmunks increased sharply in legacy mosaics following VDT and remained high. Douglas' squirrels did not respond to VDT in the short term. It remains to be seen whether flying squirrels and Douglas' squirrels will increase over time as tree diversity increases and as trees increase photosynthetic activity and allocate additional carbon to seeds and ectomycorrhizal associates. California hazel (*Corylus cornuta* Marsh var. *californica* (A. DC.) Sharp) and bigleaf maple (*Acer macrophyllum* Pursh) are present and may begin producing high quality nuts and seeds for the squirrels in response to the more open canopy and available light.

Wintering birds

Species richness was higher in timber (16.2 ± 1.4 species) than in legacy stands (12.2 ± 1.0 species). Richness remained unchanged in timber mosaics, ranging from 14 to 22 species 3-5 years after VDT. Richness varied annually but was consistently higher in legacy mosaics than in legacy controls in post-VDT years 3-5 (annual richness was 12-16 species in mosaics versus 10-16 species in controls). The proportion of stand area used increased in mosaics for two of eight abundant species (*Troglodytes troglodytes* and *Melospiza melodia*). No species used legacy controls more than timber or mosaic stands. Cavity-excavating birds (Picidae) were present, but low in abundance, in all stands.

Discussion

All stands had soils heavily dominated by fungal mycelia and mycophagous nematodes and diverse communities of both epigeous and hypogeous fungi. The similarity between the fungal communities in timber and legacy stands suggests high resiliency in soil food webs in the face of active management (Carey *et al.*, 1996). Timber management, however, appeared to have reduced fungal dominance, suggesting some impacts of past management on soils, particularly on macroscopic fungal mats. Mechanical disturbance during VDT appeared to destroy fungal mats and promote *Melanogaster* over *Hysterangium* and *Gautieria*. Similar results were reported by Aguilera *et al.* (1993) and Waters *et al.* (1994). Impacts of VDT on truffle production, however, were brief. The long-term impacts of forest management on truffle production remain unclear, with inconsistent results from across the region (Carey *et al.*, 2002; Smith *et al.*, 2002). Heterogeneity induced by VDT increased sporocarp diversity to a richness that rivals that in old growth (Carey *et al.*, 2002). Retaining unthinned patches in mosaics might help conserve fungal mats and allow their recolonization as increased photosynthetic activity by trees increases the flow of carbohydrates to soil food webs and maintains high fungal diversity.

Conventional thinning produced timber stands with a rich understorey dominated by clonal natives with numerous exotics present. Achlorophyllous mycotrophs were reduced in abundance by dense understorey; retaining unthinned patches in mosaics would help conserve these species. Understoreys in the timber stands, however, lacked both shade-tolerant trees and the spatial heterogeneity associated with diverse vertebrate communities (Carey *et al.*, 1999a). Legacy forests had depauperate understoreys and low abundances of small mammals and winter birds. Thus, neither historical management regime had placed stands on a trajectory toward developing the complexity and diversity of old-growth forests. Mosaics increased diversity and abundance of native species, but only ephemerally increased exotics. Underplanting is leading to increased spatial heterogeneity. With time, it now appears

and legacy stands has been altered by VDT and that development of biocomplexity, although far from ensured, is more likely than before treatment.

Timber and legacy management produced imbalanced mammal communities, with some species common in natural forests (Carey, 1995; Carey and Johnson, 1995) low in abundance. Mosaics had immediate positive effects on forest-floor mammals, but shade-tolerant mid-storeys and midstorey deciduous trees (e.g. *Acer macrophyllum* Pursh) will be required to restore biotic integrity. Chipmunks increased markedly in legacy mosaics, with only brief declines in flying squirrels. Flying squirrels remained rare (some of the lowest densities ever recorded in the Pacific Northwest) in the timber stands, perhaps due to dense homogeneous understoreys that promoted excessively high and uniform chipmunk abundance. Similarly, mosaics had positive effects on the winter birds and increased overall habitat quality. Bird communities, however, continued to have low abundances of cavity-excavating birds. Promoting deciduous trees early in stands development provides both short-lived trees (e.g. *Alnus rubra* Bong) for cavity excavation and long-lived trees (e.g. *Acer macrophyllum* Pursh and *Arbutus menziesii* Pursh) for mammal dens (Carey *et al.*, 1997). Decadence management may prove essential to maintaining cavity-excavating birds and forest-floor organic matter in managed forest.

In summary, inducing heterogeneity into homogeneous canopies had positive effects on diverse biotic communities and ecosystem function as habitat in the short term (<5 years) in stands managed with conventional thinning for timber and with legacy retention alone. Success of underplanting will determine if heterogeneity will continue to increase and time will tell if other elements of diversity (e.g. deciduous trees, certain small mammals and certain birds) will be restored. Research is needed on managing decadence to provide cavity trees and coarse woody debris. Nevertheless, VDT shows promise as part of a holistic management approach. It seems likely that intentional management disturbance can produce spatial complexity at multiple scales, including the fine scale, that will prove important in restoring and maintaining biodiversity in

second-growth temperate, boreal and tropical forests (Canham *et al.*, 1990; Franklin *et al.*, 1997, 2000, 2002; Carey *et al.*, 1999a, b; Larsson and Danell, 2001; Korpilahti and Kuuluvainen, 2002; Lindenmayer and Franklin, 2002; Carey, 2003).

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