RESEARCH ARTICLE

Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests

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ABSTRACT

1 We expanded the island biogeography paradigm to test whether mammalian communities of the heavily fragmented temperate rain forests of the Olympic Peninsula were influenced by local environmental conditions, biogeographic factors (fragment area and isolation) and characteristics of the surrounding landscape.

2 We used live-trapping, sign surveys and infrared triggered cameras to compare distributions of non-volant mammals among fragments and between fragments and other principal landscape components (continuous old-growth, riparian corridors, second-growth forest and clearcuts).

3 Of the 24 species of non-volant mammals detected during our studies, 18 occurred in at least one fragment.

4 Species richness of old-growth mammals was not significantly correlated with fragment area or isolation, *per se*, but was significantly and positively correlated with the amount of old-growth fragments and old second-growth (41–159 years) in the surrounding landscape ($r^2 = 0.95$, $P < 0.005$).

5 Distributions of three old-growth dependent species [shrew-mole (*Neurotrichus gibbsii*), Douglas squirrel (*Tamiasciurus douglasii*) and Trowbridge shew (*Sorex trowbridgii*)] were significantly associated with local environmental conditions within the fragment, with geographical isolation from continuous old-growth and riparian corridors, and with the amount of old-growth and old second growth in the adjacent matrix.

Key words fragmentation, islands, landscape ecology, mammals, old-growth, species–area relationship, species–isolation relationship, temperate rain forests.

INTRODUCTION

The historic record of extinctions testifies to the vulnerability of isolated biotas (see summary in Brown & Lomolino, 1998, pp. 533–572). Although oceanic islands cover a relatively small fraction of the earth's surface (< 10% of the land surface), a highly disproportionate number of species extinctions during the past 400 years have been insular. In more recent times, however, the rate of extinctions on the continents has increased to the point where it now rivals that on islands (see Lomolino & Channell, 1995; their Fig. 1). Yet these continental extinctions may still be viewed as insular phenomena. Once-expansive, continuous stands of old-growth forests, prairies and other native ecosystems have been reduced to ever-dwindling archipelagos of habitat islands, each isolated by a complex mixture of intervening habitats often referred to as the habitat matrix.

The heterogeneity of these anthropogenic landscapes poses some particular challenges to ecologists and conservation biologists attempting to apply island biogeography theory to understand and conserve biological diversity in fragmented landscapes. Certainly, the most commonly used

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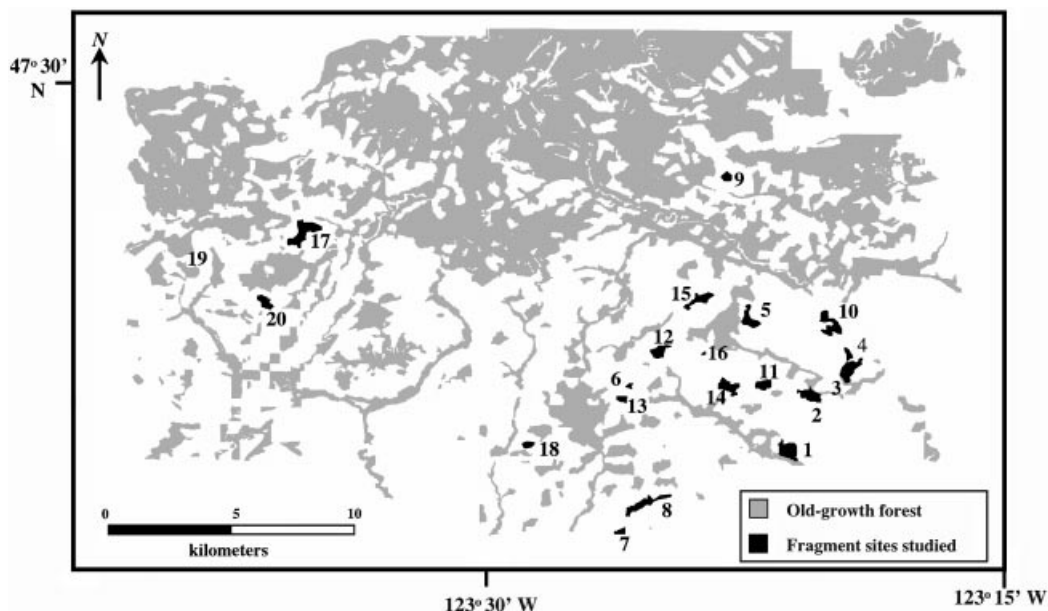
Fig. 1 Map of the Hoodsport District of Olympic National Forest, Washington, USA, showing old-growth forest habitats (grey) and the 20 fragments studied (black). Numbers correspond to the site numbers in Table 2.

tools of this field, particularly the species–area relationship and the equilibrium theory of MacArthur & Wilson (1967), may provide some useful insights (e.g. Harris, 1984; Shafer, 1990; Doak & Mills, 1994); yet they fail to take into account the complexity of these continental archipelagos. Oceanic archipelagos are viewed typically as collections of ecosystems varying in area and isolation, but assumed to be similar in their habitat conditions, and to be situated within a relatively homogeneous sea of intervening waters. In contrast, fragmented continental ecosystems are highly variable in space and time. In addition to their marked decline in continuity, anthropogenically fragmented systems often exhibit appreciable variation in habitat conditions from one fragment to the next and across portions of the intervening matrix, which often is in a state of flux or relaxation (decline from a more diverse community) from some previous disturbance. This complexity probably exceeds the conceptual bounds of the traditional island paradigm. However, given some key insights from community and landscape ecology, this paradigm

may be broadened to provide a more powerful tool for understanding and hopefully conserving the diversity of native biotas inhabiting now-fragmented ecosystems.

Our purpose here is to evaluate the utility of this more inclusive island paradigm by studying patterns of spatial variation in vertebrate community structure across a heavily fragmented landscape. Specifically, we test the predictions that species richness and species composition of non-volant mammals in fragments of a temperate rain forest are significantly correlated with biogeographic parameters (namely fragment area and isolation), landscape composition (i.e. relative proportion of different habitats in the adjacent matrix) and habitat characteristics of the fragments. Our studies were conducted in the fragmented, old-growth forests of the Olympic Peninsula, Washington (Fig. 1), which was also the site of a set of related studies on the effects of anthropogenic landscape transformation on temperate rain forest mammals (see Songer *et al.*, 1997; Perault, 1998; Lomolino & Perault, 2000; Perault & Lomolino, 2000).

METHODS

Site description

We conducted analyses across the Hood Canal District (approximately 60 000 ha) of the Olympic National Forest in north-west Washington. Due to its relatively stable, wet and relatively cool but equable climate, the prehistoric landscape of the Olympic Peninsula has changed little over the past five or six millennia (see Brubaker, 1991; Whitlock, 1992). In contrast to its temporal stability, this region is comprised of a spatially heterogeneous mixture of native landscapes that vary in concert with its steep elevation gradients (Peterson *et al.*, 1997). The Olympic Mountains, which lie near the centre of the peninsula, rise rapidly from sea level to just under 2800 m. Below the mountain peaks lies an equally steep vegetational gradient characterized by a juxtaposition of distinct life zones ranging from alpine tundra down to lowland, temperate rain forests (0–1000 m above sea level).

Prior to settlement, lowland rain forest was the peninsula's most expansive life zone and was dominated by nearly continuous, old-growth stands of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja pilicata*; see Norse, 1990). In the absence of major fires, hurricanes and other significant natural disturbances, these old-growth forests continued to dominate the lowland areas until the 1940s. Subsequent technological advances of the timber industry, however, led to a rapid and dramatic change in the landscapes across the peninsula. Continuous old-growth forests were replaced by clearcuts, monospecific, even-age stands of second-growth forests, and an archipelago of hundreds of forest fragments that vary substantially in their size, shape and habitat characteristics (Fig. 1; see also Rosenberg & Raphael, 1990).

Old-growth forest in this region consists of stands having the following characteristics: eight trees per acre older than 160 years or more than 32 inches (81.3 cm) diameter-at-breast-height (d.b.h.), deep multi-layered canopy with at least four conifer snags of at least 20 inches (50.8 cm) d.b.h., and at least 20 tons of logs per acre greater than 23 inches d.b.h. and at least 15 m long (Old-growth Definition Task Group, 1986). Fragmentation of the once-dominant old-growth forest has steadily increased from 1900 to 1990

(see Fig. 17.22-c in Brown & Lomolino, 1998). Particularly since the 1950s, well over half of the mature forests in this district have been logged.

The principal landscape components of Olympic National Forest now include the following macrohabitats:

1 Old-growth forest (age-class > 160 years), further broken down into:

(a) continuous forest: areas of old-growth forest > 50 km²;

(b) fragments: patches of old-growth forest of 0.1–2 km² and separated completely from old-growth forests by clearcuts or successional habitats; and

(c) corridors: linear bands of old-growth forest < 1 km across at their greatest width, > 8 km in length, and connected to continuous forest.

2 Second-growth forest: stands of monospecific, even-age class trees, 26–80 years following harvesting.

3 Clearcut: sites < 26 years following harvesting, with an absence of trees > 3 m in height and > 3 cm d.b.h.

Field methods

In two previous studies we analysed differences in mammalian community structure among the above five macrohabitats (Lomolino & Perault, 2000) and assessed the ecological role of riparian corridors (Perault & Lomolino, 2000). Here we report on the results of biological surveys conducted in 20 fragments of the Hood Canal District during the summers (June–August) of 1994–97. The fragments we studied were selected such that they occurred across the extent of the district (Fig. 1). They included an appreciable and representative range in isolation and area, but these independent variables were not significantly correlated.

Each continuous forest site contained five survey stations. Depending on its size, each fragment had two to five stations, and each corridor had four stations, two in old-growth forest paired with two in the adjacent second-growth or clearcut. Stations were spaced 75 m apart and were situated at least 75 m from the nearest forest edge.

At each station, live-traps (pitfalls, Shermans and Tomahawks), infra-red triggered cameras and sign surveys were used to detect local mammals. Live-trapping surveys took place over a 5-day pre-bait period followed by 7 days of trapping.

Table 1 Habitat variables measured at each station, Hood Canal District, Olympic National Forest, Washington

Abbreviation	Description
DTOP	Canopy height (measured with a clinometer)
CANC	Canopy closure (measured with a spherical densiometer)
Edge	Distance to nearest edge (forest or clearcut)
Slope	Percentage of slope (measured with a clinometer)
Snag	Number of snags present in a 10-m radius
T20,T20–40,T40	Number of trees with a d.b.h. of < 20 cm, 20–40 cm, and > 40 cm, respectively, in a 10-m radius
L20,L20–40,L40	Number of logs with a d.b.h. of < 20 cm, 20–40 cm, and > 40 cm, respectively, in a 10-m radius
S20,S20–40,S40	Number of stumps with a d.b.h. of < 20 cm, 20–40 cm, and > 40 cm, respectively, in a 10-m radius
Moss	Frequency of moss at 22 points in plot
Fern	Frequency of ferns at 22 points in plot
Grass	Frequency of grass at 22 points in plot
Rock	Frequency of rock at 22 points in plot
Shrub	Frequency of shrub at 22 points in plot
Herb	Frequency of herb at 22 points in plot
Litter	Frequency of litter at 22 points in plot
Soil	Frequency of exposed soil at 22 points in plot

Live-traps were set within a 6-m radius of the station centre and in a variety of available microhabitats. Five 2-litre pitfall traps, four Sherman live-traps (one $4.0 \times 4.5 \times 15''$ and three $3.0 \times 3.0 \times 9''$) baited with peanut butter and oats, one chipmunk-sized ($5 \times 5 \times 16''$) and one squirrel-sized Tomahawk live-trap ($6 \times 6 \times 24''$) baited with raw chicken, cracked corn, apples, carrots and peanut butter were set at each station. The pitfalls were placed along a line approximately 1 m apart near the periphery of each trap station. Sherman traps were placed along the four cardinal directions at approximately 5 m from the station centre. Tomahawk traps were set within 6 m of the station centre and located near stumps, logs and trees. The traps were locked open for the 5-day pre-bait session, then unlocked, re-baited, and checked daily for the next 7 days. All small mammals captured were weighed, measured, sexed, aged, marked by toe clipping and released. Relative frequencies for each trapped species were determined by dividing the number of individuals captured (excluding recaptures) by the number of functional trap-nights. Functional trap-nights were calculated by subtracting from the total potential number of trap-nights,

1.0 for traps that were not functional, and 0.5 for traps that were disturbed, missing bait, or contained a recaptured individual (Songer *et al.*, 1997).

In addition to live-trapping, infra-red triggered cameras and sign surveys were used to detect the presence of larger or more secretive species. One camera station was established between every two trapping stations and no closer than 75 m from the nearest trap stations. Camera stations were baited with raw chicken, peanut butter and oats and cracked corn, and were run for the duration of each 12-day trapping session. Sign surveys were also conducted throughout each session by searching for scats, tracks, feeding signs and dens within and along the 75-m paths between trap stations.

Geographic, landscape and habitat characteristics

At each trap station, 22 environmental characteristics were recorded during the trapping session (Table 1). Two 10-m ropes, knotted at 1-m intervals, were placed along the cardinal directions crossing at 90° angles at the centre of the

site. Under each knot we recorded the presence of litter, rock, fern, moss, herbaceous plant, shrub, stump, log or tree. Also, the number of snags and size of trees, logs and stumps were counted within a 10-m radius of the plot centre. Size categories included trees, stumps and logs that were < 20 cm d.b.h., between 20 and 40 cm d.b.h. and > 40 cm d.b.h. Canopy closure was measured with a spherical densiometer. A clinometer was used to estimate slope and canopy height. The distance from the site to the nearest edge of the macrohabitat was also recorded.

In addition to fragment area, we measured the geographical isolation, landscape composition and habitat characteristics of each fragment using the GIS program ARC/INFO (Environmental Systems Research Institute, 1997; Table 2). We first measured geographical isolation as the straight-line distance from the edge of a fragment to the nearest edge of a corridor or continuous old-growth forest (NNCFCOR, Table 2). We also measured geographical isolation along a path from the fragment to continuous old-growth that would minimize distance travelled through clearcuts (OPTPATH). Our measures of landscape impedance (resistance of different land-covers to movements by target species) were based on the percentages of the surrounding landscape within 1 km of the fragment that was classified as continuous old-growth forests and corridors (CFCO1000), old-growth fragments (FR1000), old second-growth (49–159 years; OS1000) or young second-growth and clearcuts (YSCC1000). As the percentage of old-growth and old second-growth increases, landscape impedance (resistance to movement by old-growth species) decreases.

Statistical analyses

Analyses of patterns in community structure were conducted separately for old-growth-dependent species ($N = 8$) and other species of mammals ($N = 10$; see list of species in Table 3). The list of old-growth forest species was determined a priori based on information on habitat associations available in the literature (primarily Larrison & Fisher, 1976; Norse, 1990; Carey & Johnson, 1995). Consistent with this designation, our other, concurrent studies in this region (Lomolino & Perault, 2000) indicated that all eight of these

species occurred much more frequently and at much higher densities in continuous old-growth and corridors in comparison to second-growth and clearcuts. Three of these species [Northern flying squirrel (*Glaucomys sabrinus*), shrew-mole, and Pacific water shrew (*Sorex bendiri*)] were never detected in clearcuts.

Principal Components Analysis was used to reduce the set of 22 measured habitat variables (Table 1) to four composite variables that summarized the overall variation in habitat among fragments (Table 2, FHAB1–4; SYSTAT 1997). The variation explained by these components was 21.4, 18.1, 13.2 and 8.3%, respectively. Pearson product–moment correlations were used to assess the covariation among independent variables. Eight of the 45 correlation coefficients were significant ($P < 0.05$; bold entries in Table 4) in simple comparison, but none of these were significant after adjusting for multiple comparisons (Dunn–Sidak correction probabilities > 0.14).

Linear regression was used to analyse the species–area relationship for the 20 fragments studied (using the power model, fixed model, with log-transformations for area and isolation; SYSTAT 1997). Two separate regressions were conducted — one for old-growth-dependent species and one for other species of mammals. In addition, stepwise regression analysis was used to investigate the association between species richness and biogeographic variables [fragment area and isolation (AREA, OPTPATH, NNCFCOR), habitat within a fragment (FHAB1–4) and characteristics of the adjacent matrix (OS1000, FR1000 and YSCC1000; alpha-to-enter and alpha-to-stay were set to 0.15 and 0.05, respectively]. One case (fragment 9) was deleted from the stepwise regression due to its undue influence on regression estimates (leverage ≥ 0.65; SYSTAT 1997).

Patterns of distributions of individual species among old-growth fragments were analysed using discriminant function analysis (see previous descriptions of these methods in Lomolino, 1986 and Lomolino *et al.*, 1989). Analyses were conducted only for those species occurring in between five and 20 fragments. The dependent, or grouping, variable was presence or absence of the species, and independent variables included fragment area, geographical isolation (NNCFCOR and OPTPATH), fragment habitat (FHAB1 and FHAB2) and landscape characteristics (OS1000

Table 2 Geographic, landscape and environmental characteristics for each of the old-growth forest fragments surveyed during the Summers of 1994–97 in the Hoodsport District of the Olympic National Forest, Washington, USA (see Fig. 1)

Fragment no.	Biogeographic variables			Landscape variables				Environmental, within fragment			
	AREA (ha)	NNCFORCO (m)	OPTPATH (m)	CFCO1000 (%)	OS1000 (%)	FR1000 (%)	YSCC1000 (%)	FHAB1	FHAB2	FHAB3	FHAB4
1	39.84	6033.3	21658.8	0.0	37.2	15.3	23.8	−0.716	−1.537	−0.408	0.687
2	30.63	4391.5	15232.7	0.0	49.9	11.9	36.3	−0.777	−1.073	0.327	−1.238
3	38.64	3037.3	16969.3	0.0	49.0	12.5	13.9	−1.386	−1.200	−1.213	−0.337
4	7.55	2328.0	17898.8	0.0	40.3	12.7	24.3	−0.877	−0.928	0.148	1.525
5	27.61	2055.7	8972.6	0.0	12.6	29.2	58.1	−1.201	0.784	1.889	0.162
6	3.11	861.9	14566.4	1.1	27.9	6.5	64.5	−2.227	1.678	0.198	1.294
7	6.12	1522.9	18221.8	0.0	5.2	2.3	10.5	−0.293	0.099	1.428	−1.194
8	34.90	1327.5	17327.9	0.0	14.1	7.1	53.1	−0.760	−0.683	0.004	−0.887
9	9.99	509.5	509.5	27.1	8.8	0.5	62.3	1.036	0.919	−0.733	−0.545
10	39.73	1198.4	9821.0	1.0	46.7	0.6	36.3	0.541	0.078	−0.081	1.097
11	18.80	4453.0	12783.6	0.0	23.2	10.7	65.9	0.998	1.145	0.487	0.687
12	21.37	2058.3	11602.5	0.0	27.8	12.3	59.7	1.003	−0.548	0.386	−0.499
13	7.39	483.2	12552.2	13.5	16.5	2.1	67.8	0.733	0.529	−0.556	0.570
14	29.47	4113.0	12285.5	0.0	26.2	7.4	66.2	1.263	0.439	0.529	1.410
15	23.36	1135.0	6497.0	1.1	21.2	10.1	67.5	0.466	0.123	−0.789	−1.520
16	0.93	3398.6	10823.2	0.0	15.5	19.4	65.1	−0.588	1.901	−2.530	−0.831
17	58.91	678.1	3028.4	11.1	26.0	16.4	45.9	0.404	0.699	1.677	−1.563
18	9.11	603.8	10747.0	6.7	21.2	14.6	57.4	0.798	−0.582	−0.147	0.408
19	44.97	569.3	7324.8	6.7	33.1	7.1	52.5	0.871	−1.234	−0.203	0.074
20	18.09	1897.4	6828.9	0.0	23.5	26.2	31.6	0.713	−0.607	−0.412	0.701

NNCFORCO Straight-line distance to nearest continuous forest or old-growth corridor. OPTPATH Total distance along a path from the fragment to nearest continuous forest which minimize distance through clearcuts. CFCO1000 Percent of landscape within 1000 m of the fragment covered by either continuous forest or old-growth corridor. OS1000 Percent of landscape within 1000 m of the fragment covered by old (41–159 years) second growth forest. FR1000 Percent of landscape within 1000 m of the fragment covered by forest fragments. YSCC1000 Percent of landscape within 1000 m of the fragment covered by either young second growth (26–40 years) or clearcuts (< 26 years). FHAB1–4 First four scores from principal components analysis of 22 environmental variables at each station (see Table 1). FHAB1 increases with canopy closure, litter, and density of large (> 40 cm diameter) trees, stumps and logs. FHAB2 increases with frequency of snags, slope angle, and frequency of small (< 20 cm diameter) stumps and logs. FHAB3 increases with frequency of small (< 20 cm diameter) trees, but decreases with frequency of shrubs. FHAB4 increases with density of herbaceous vegetation and with distance from fragment edge, but decreases with coverage of moss. Percentage of variance in environmental variables explained = 21.4, 18.1, 13.2 and 8.3%, respectively.

Table 3 Results of mammal surveys conducted in 20 old-growth fragments of the Hoodsport District of Olympic National Forest, Washington, during the summers of 1994–97. Data presented are occurrence of species (1 = present, 0 = absent) based on live-trapping, sign and infra-red triggered camera surveys for these species (see species codes below)

Fragment site	Old-growth forest species (in bold)†								Matrix species									
	PEOR	**CLGA**	**SOMO**	**SOTR**	**TADO**	**NEGI**	**GLSA**	**SOBE**	PEMA	TATO	ODHE	SPPUsi	URAM	MUER	APRU	SOVA	LYRU	MILO
1	1	1	1	1	0	1	0	0	1	1	0	1	0	0	1	0	0	0
2	1	1	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0
3	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0
4	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0
5	1	1	1	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0
6	1	1	1	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0
7	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0
8	1	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0
9	1	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	1	0
10	1	1	1	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0
11	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
12	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
13	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
15	1	1	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0
16	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
17	1	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0
18	1	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
19	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0
20	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0
Incidence	20	17	16	12	11	5	3	1	12	11	7	6	6	5	4	3	2	1

Species codes (methods of detection; T = live trapping, C = infrared triggered camera, and S = survey for animal signs):
PEOR = Forest deermouse, *Peromyscus oreas* (TC); **CLGA** = Red-backed vole, *Clethrionomys gapperi* (TC); **SOMO** = Montane shrew, *Sorex monticolus* (T); **SOTR** = Trowbridge shrew, *Sorex trowbridgii* (T); **TADO** = Douglas squirrel, *Tamiasciurus douglasii* (TCS); **NEGI** = Shrew-mole, *Neurotrichus gibbsii* (T); **GLSA** = Northern flying squirrel, *Glaucomys sabrinus* (TC); **SOBE** = Pacific water shrew, *Sorex bendirii* (T); PEMA = Common deermouse, *Peromyscus maniculatus* (TC); TATO = Townsend chipmunk, *Tamias townsendii* (TC); ODHE = Mule deer, *Odocoileus hemionus* (CS); SPPU = Spotted skunk, *Spilogale putorius* (TC); URAM = Black bear, *Ursus americanus* (CS); MUER = Short-tailed weasel, *Mustela erminea* (TC); APRU = Mountain beaver, *Aplodontia rufa* (CS); SOVA = Vagrant shrew, *Sorex vagrans* (T); LYRU = Bobcat, *Lynx rufus* (CS); MILO = Long-tailed vole, *Microtus longicaudus* (T).
† List of old-growth dependent species was determined a priori based on habitat associations described in the literature (primarily Larrison & Fisher, 1976; Norse, 1990; Carey & Johnson, 1995; see Wilson & Reeder, 1993 for sources of sceintific names).

Table 4 Pearson product–moment correlations among 10 environmental, geographical and landscape variables measured at each old-growth fragment. Values in bold were statistically significant at the 0.05 level†

	FHAB1	FHAB2	FHAB3	AREA	NNCFORCO	OPTPATH	CFCO1000	OS1000	FR1000
FHAB2	0.000								
FHAB3	0.000	0.000							
AREA	0.089	−0.429	0.289						
NNCFORCO	−0.179	−0.198	−0.101	0.126					
OPTPATH	**−0.546**	−0.389	0.000	−0.111	**0.546**				
CFCO1000	0.400	0.227	−0.091	−0.072	**−0.508**	**−0.623**			
OS1000	−0.218	**−0.538**	−0.124	**0.455**	0.374	0.308	−0.342		
FR1000	−0.225	−0.049	0.083	0.094	0.286	−0.073	−0.375	−0.006	
YSCC1000	0.350	**0.606**	−0.119	−0.228	−0.242	**−0.489**	0.300	−0.427	−0.060

† None of these correlations were significant after correcting for multiple comparisons (Dunn-Sidak probabilities > 0.14).

and FR1000). The analyses were conducted using the GLM module of SYSTAT (1997; alpha-to-enter and alpha-to-stay were set to 0.15 and 0.05, respectively; model run without a constant).

RESULTS

General patterns in species composition

Although we detected 24 species of non-volant mammals across various components of this landscape (including continuous old-growth, old-growth corridors, fragments, second growth or clearcut), six species were not detected in any of the 20 fragments we studied [long-tailed weasel (*Mustela frenata*), elk (*Cervus elaphus*), Pacific jumping mouse (*Zapus trionatus*), coyote (*Canis latrans*), bushytail woodrat (*Neotoma cinerea*) and snowshoe hare (*Lepus americanus*); see Lomolino & Perault, 2000]. Long-tailed weasels were only detected at one clearcut site, while the remaining five species were detected in at least one of the continuous forest sites. Elk and snowshoe hares were also detected in corridors and clearcuts, and western jumping mice were also detected in clearcuts.

Of the 18 species detected in old-growth fragments (Table 3), rodents and insectivores were by far the most frequently detected species, with forest deermice (*Peromyscus oreas*) occurring in all 20 fragments, followed by red-backed voles (*Clethrionomys gapperri*) in 17 fragments, montane shrews (*Sorex monticolus*) in 16, Trowbridge shrews (*S. trowbridgii*) and common deermice (*P. maniculatus*) in 12, and Douglas squirrels (*Tamiasciurus douglasii*) and Townsend chipmunks (*Tamias townsendii*) in 11 fragments.

Patterns in species richness

Species richness varied from one to eight for old-growth dependent species and from zero to five for other species of mammals. Despite the range in richness among fragments, univariate regression analysis failed to yield a significant species–area relationship for either group of mammals [old-growth dependent or otherwise; log-log (power) model, $P > 0.10$, $r^2 < 0.10$; Table 5, Fig. 2].

Multiple regression analyses, however, revealed that species richness of old-growth dependent mammals was significantly correlated with two

Table 5 Results of regression analyses of the relationships between species richness of old-growth dependent species and other mammals as a function of environmental, geographical and landscape variables (those reported in Table 2)

Effect	Regression coefficient (b)	Standard error	*t*-value	*P*-value (two-tailed)	Adjusted r^2
Power model, species–area relationship [Log(s) vs. Log(A)]					
Richness of old-growth-dependent species (*N* = 20):					0.07
Constant	−0.1535	0.4892	−0.314	0.7573	
$Log_{10}(A)$	0.1434	0.0935	1.535	0.1422	
Richness of other species (*N* = 20)					0.05
Constant	−0.4262	0.6021	−0.708	0.4886	
$Log_{10}(A)$	−0.1634	0.1146	1.425	0.1721	
*Stepwise regression analyses of richness and variables listed in Table 2**					
Richness of old-growth dependent species (*N* = 19)†					0.95
OS1000	0.10415	0.01214	8.579	< 0.0001	
FR1000	0.11753	0.02613	4.499	0.0003	
Richness of other species (*N* = 19)†					0.96
AREA	0.000007	1E−06	7.187	< 0.0001	
OPTPATH	0.000144	2.9E−05	4.952	0.0017	
FHAB1	−0.71214	0.18851	−3.778	0.0018	
NNCFORCO	−0.000308	0.00013	−2.379	0.0311	

* Alpha to enter and remove = 0.15 and 0.05, respectively; model does not include a constant. † One case (fragment 9) was deleted due to its undue influence on regression estimates (leverage > 0.65).
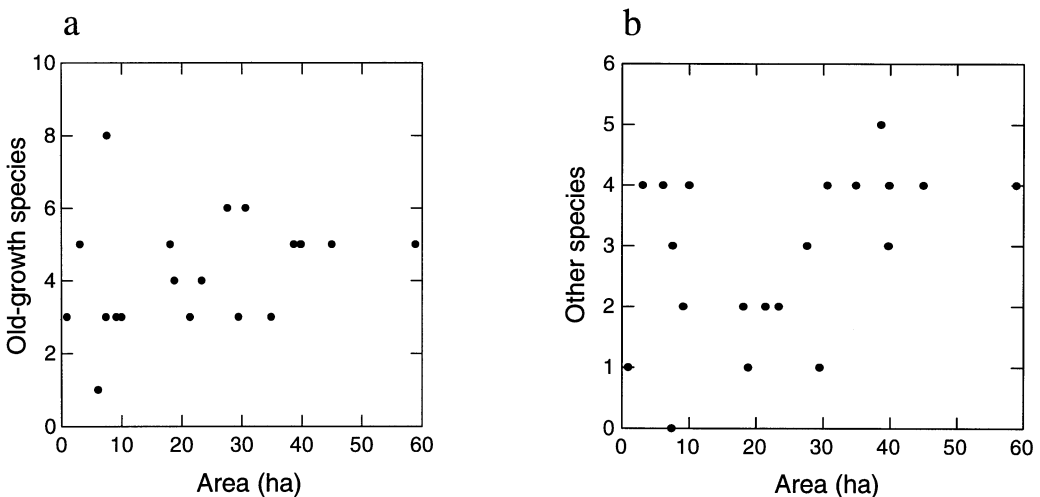
Fig. 2 Species–area relationships for old-growth forest mammals (a) and for other (matrix) species (b) inhabiting fragments of the Hoodsport District of Olympic National Forest, Washington, USA (see Table 4 for list of species).

measures of landscape isolation, or what Perault & Lomolino (2000) have termed landscape impedance (P < 0.001, r^2 = 0.95; Table 5). Richness of these species was highest for fragments surrounded by a matrix that included relatively high cover of fragments and old second growth (41–159 years; i.e. fragments situated within a matrix of relatively low impedance; see Fig. 3a).

Table 6 Results of stepwise discriminant analysis of factors influencing the occurrence of mammals within forest fragments of the Hoodsport District of the Olympic National Forest, Washington. Analyses conducted only for the seven variables listed and for those species occurring on between five and 15 of the 20 fragments studied

| Species | Incidence | r^2 | P-values (includes only those < = 0.05) | | | | | | |
| | | | | Geographic isolation | | Landscape impedance | | Habitat within fragments | |
			Area	NNCFCOR	OPTPATH	OS1000	FR1000	FHAB1	FHAB2
Old-growth-dependent species									
Neurotrichus gibbsii	5	0.78				0.0001		0.0498	0.0008
Tamisciurus douglasii	11	0.61					0.0001		
Sorex trowbridgii	12	0.78		0.0392		0.0004	0.0387		
Other species									
Eutamias townsendii	11	0.74	< 0.0001					0.0028	
Odocoileus hemionus	7	0.53	0.0004						0.0484
Ursus americanus	6	0.59	0.0235		0.0252		0.0217		
Peromyscus maniculatus	12	0.77					< 0.0001		0.0317
Spilogale putorius	6	0.45			0.0009				
Mustela erminea	5	0.29			0.0127				

Area: fragment area. NNCFORCO: Straightline distance to nearest continuous forest or old-growth corridor. OPTPATH: Total distance along a path from the fragment to nearest continuous forest which minimizes distance through clearcuts. FR1000: percent of landscape within 1 km that is covered by other fragments. FHAB1, 2: First two-factor scores from principal componenets analysis of habitat variables reported in Table 1. FHAB1 increases with canopy closure, litter and density of large (> 40 cm diameter) trees, stumps and logs. FHAB2 increases with frequency of snags, slope angle and frequency of small (< 20 cm diameter) stumps and logs.

Multiple regression analyses also indicated that richness of other species of mammals (i.e. matrix species) was significantly correlated with measures of geographical isolation (or proximity to old-growth forests), fragment habitat and fragment area ($P < 0.05$, $r^2 = 0.96$; Table 5). Richness of these species tended to increase with increasing distance along an optimal path to continuous old-growth forests (OPTPATH), with increased fragment area (Fig. 3b), and with decreased degree of old-growth characteristics (FHAB1, which increases with increasing canopy closure, litter and density of large trees, stumps and logs; Fig. 3c).

Note that what may at first seem to be an anomalous pattern, richness *increasing* with a measure of geographical distance (OPTPATH), is actually consistent with the assumption that sources for these matrix species are clearcuts and early second-growth forests. That is, OPT-PATH is an inverse measure of isolation for these species. Also note that, contrary to the results of univariate regression analysis (i.e. the power model for the species–area relationship), area was significantly correlated with richness of matrix species in the multivariate model ($P < 0.001$; Table 5; Fig. 3b). Finally, the surface plots of Fig. 3b,c suggest that richness of these species may result from interactive effects of these variables. For example, richness of matrix species increased with area if fragments were located close to old-growth forests (fragments with low values of OPTPATH), whereas further from these old-growth stands the species–area relationship was polytonic — first decreasing and then increasing. Similarly, the relationship between richness of matrix species and straight-line distance from continuous old-growth and corridors (NNCFCOR) appears to differ depending on the habitat characteristics of the fragment: decreasing for fragments with high old-growth development (FHAB1), but increasing with distance for those with relatively low old-growth development.

Distributions of particular species

Of the nine species occurring on between five and 15 of the 20 fragments studied, three (shrew-mole, Douglas squirrel and Trowbridge shrew) were old-growth-dependent species. Stepwise discriminant analyses indicated that distributions of these three species were not significantly influenced by fragment area (Table 6). Again this appears anomalous, but is consistent with regression analyses of the species–area relationship for old-growth-dependent species.

Incidence of all three of these species increased with increasing cover of old second-growth and old-growth fragments in the surrounding matrix (OS1000 and FR1000, respectively; Fig. 4a–c). In addition, shrew-moles occurred more frequently in fragments with relatively high canopy closure, litter and density of large trees, stumps and logs (FHAB1), but with low frequency of snags and small stumps and logs (i.e. it rarely occurred in forest gaps; FHAB2; Fig. 4a). Trow-bridge shrews occurred most frequently in fragments with both low geographical isolation (NNCFORCO) and low impedance (i.e. high levels of OS1000 and FR1000; Fig. 4c).

In contrast to the above results for old-growth-dependent species, distributions of three of the six matrix species analysed were significantly and *positively* associated with fragment area (Townsend chipmunk, mule deer and black bear; Table 6; Fig. 5a–c). Townsend chipmunk occurred more frequently in fragments with relatively low levels of old-growth conditions (low canopy closure and low densities of large trees, stumps and logs; i.e. FHAB1; Fig. 5a). Mule deer occurred most frequently in fragments with high densities of snags and small stumps and logs — i.e. in forest gaps (FHAB2; Fig. 5b). Black bear was more frequently detected in fragments that were relatively close to continuous old-growth, corridors and fragments (variables OPTPATH and FR1000; Fig. 5c).

Distributions of deer mice were significantly associated with both landscape impedance and with habitat conditions, tending to be most common in fragments that were both close to other fragments (high values of FR1000) and that included few snags and few small stumps and logs (low values for FHAB2; Fig. 5d). Distributions of the two remaining species, spotted skunks (*Spilogale putorius*) and short-tailed weasels (*Mustela erminea*), were significantly associated with geographical distance along an optimal path to continuous old-growth forests (OPTPATH; Fig. 5e,f). Both species tended to occur more frequently in fragments that were farther from
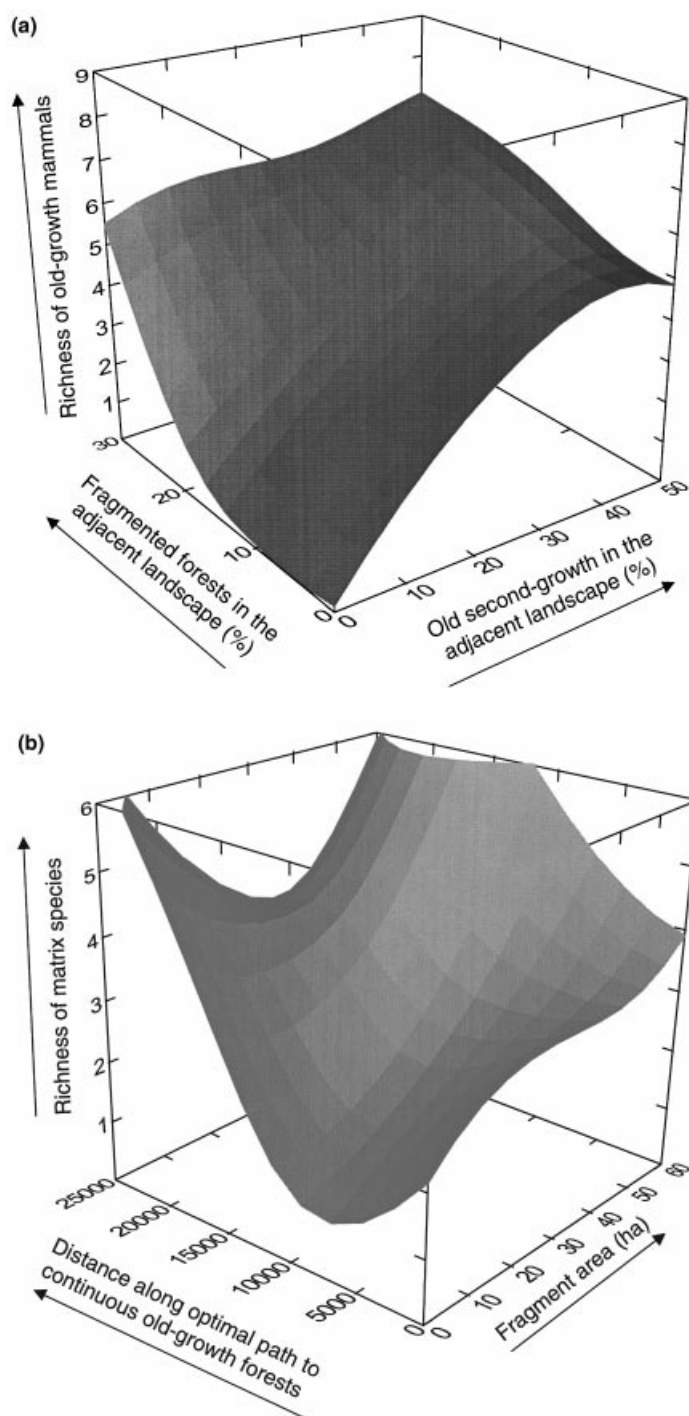
Fig. 3a Species richness of old-growth forest mammals as a function of landscape impedance, which is inversely related to the coverage of old-growth fragments and old-second growth (41–159 years) within 1 km of the fragment. (b) and (c) Richness of matrix species as a function of geographical isolation, fragment area and habitat conditions within fragments (see Tables 2 and 5).
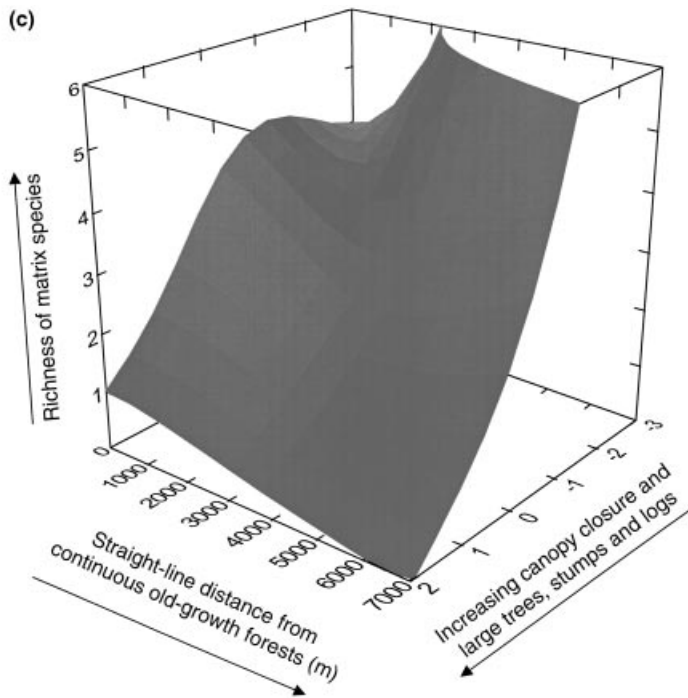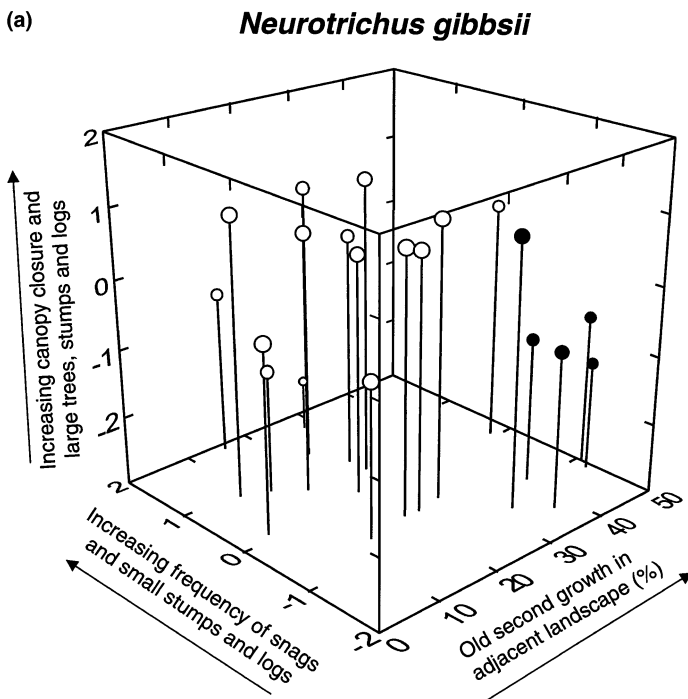
(c)

Richness of matrix species

Straight-line distance from continuous old-growth forests (m)

Increasing canopy closure and large trees, stumps and logs

Fig. 3 *continued.*

(a)

Neurotrichus gibbsii

Increasing canopy closure and large trees, stumps and logs

Increasing frequency of snags and small stumps and logs

Old second growth in adjacent landscape (%)

Fig. 4 Distributions of three old-growth forest mammals as a function of characteristics of the fragments and intervening landscape. Presence and absence within a fragment are indicated by filled and open circles, respectively (see Table 6).

(b)

Tamiasciurus douglasii

(c)

Sorex trowbridgii
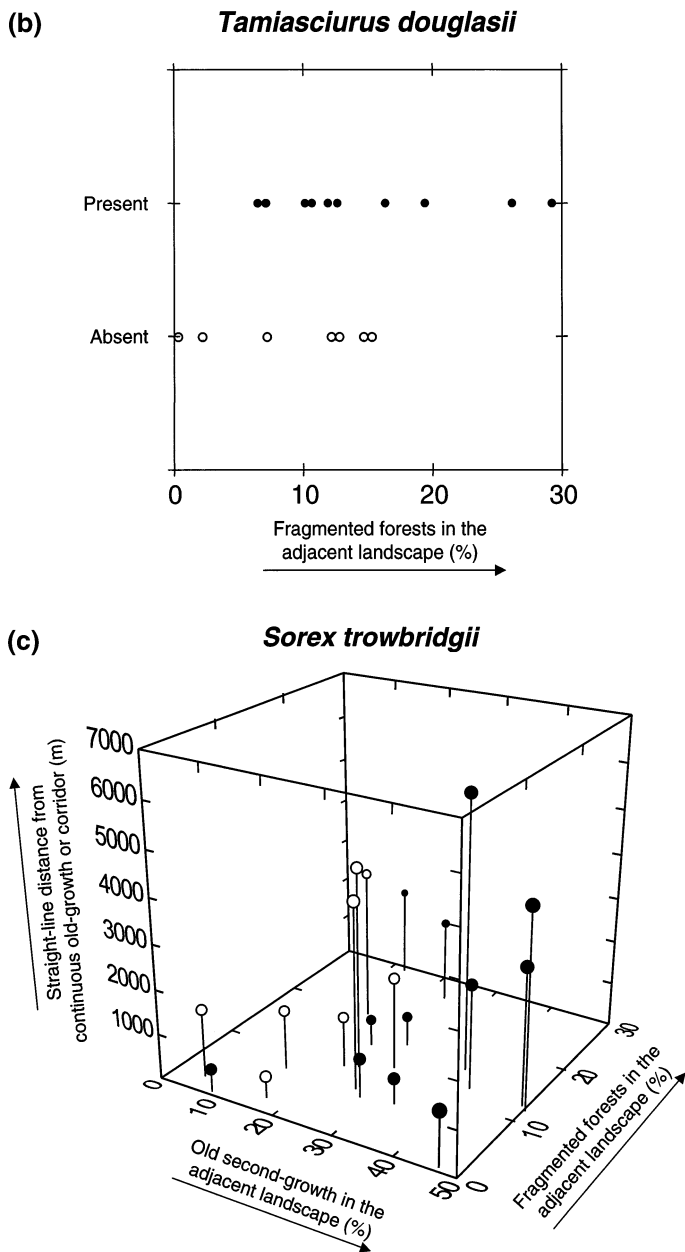
Fig. 4 *continued.*

continuous old-growth forests and corridors, but this relationship was relatively weak for short-tailed weasels ($r^2 = 0.29$ vs. 0.45 for short-tailed weasels and spotted skunks, respectively; Table 6).

DISCUSSION

Despite the existing complexity of this anthropogenically transformed landscape, patterns in variation of its mammalian communities are clear and

(a) *Eutamias townsendii*

(b) *Odocoileus hemionus*

(c) *Ursus americanus*
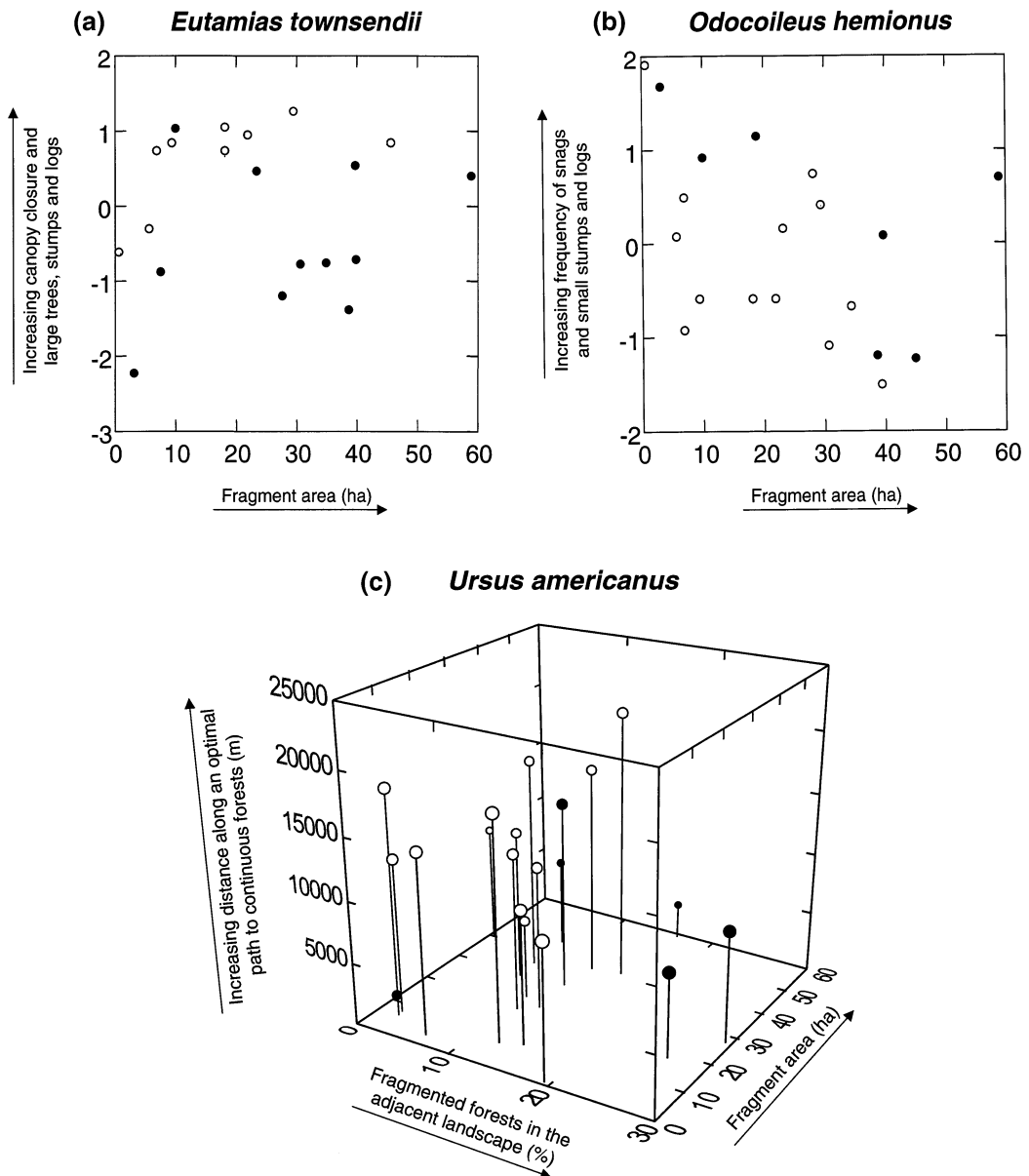
Fig. 5 Distributions of six matrix species of mammals as a function of characteristics of the fragments and intervening landscape. Presence and absence within a fragment are indicated by filled and open circles, respectively (see Table 6).

interpretable. Yet, without accurate land-cover maps and modern GIS and statistical tools, community structure and biogeography of mammals would probably appear entirely anomalous. For example, our results were inconsistent with two of the primary predictions of the reigning paradigm of biogeography — MacArthur & Wilson's (1967) equilibrium theory. Species

(d)   *Peromyscus maniculatus*

(e)   *Spilogale putorius*

(f)   *Mustela erminea*
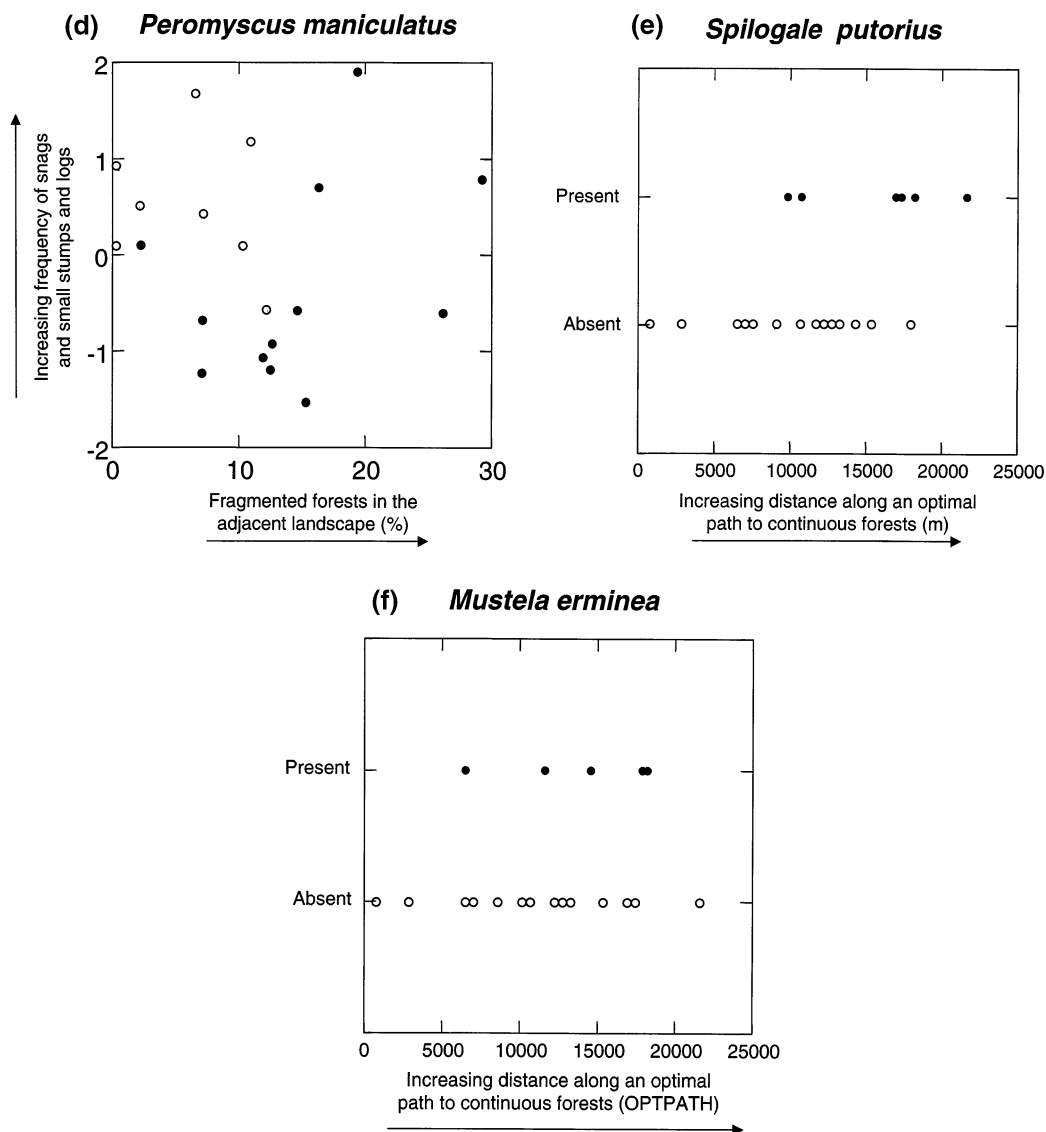
Fig. 5 *continued.*

richness of old-growth forest mammals was not correlated with fragment area or with simple geographical measures of isolation. The need to broaden the equilibrium theory, and its applications to conservation biology, becomes difficult to deny. Unlike their oceanic counterparts, the matrix of habitats isolating fragmented forests is far from homogeneous. This is the fundamental tenet of landscape ecology. Landscape heterogeneity can be demonstrable, but tractable and, as we have shown for mammals of this fragmented temperate rain forest, can account for a substantial portion of observed spatial variation in community structure. It is not that isolation and immigration are unimportant, just that landscape impedance may be a much better measure of immigration potential than more traditional measures of geographical isolation.

In a similar sense, the traditional paradigm should be broadened to include the potential influence of variation in habitat within as well as among fragments. Although richness of old-growth-dependent mammals was not significantly associated with habitat conditions of fragments, richness of other mammals (matrix species) was. Further, incidences of one of three old-growth species, and three of six matrix species were significantly correlated with fragment habitat.

The lack of a significant species–area relationship for old-growth forest mammals is an anomaly, but an important and perhaps paradoxically common one. While conservation biologists have placed much emphasis on questions related to area (e.g. see summary by Shafer, 1990; see also Holmes, 1996; Wardle & Zackrisson, 1997), a limited but possibly important body of theory and empirical studies raises a flag of caution. Granted, over a broad range of area, richness will increase with fragment size roughly in the same manner observed for most isolated ecosystems. However, the domain of most conservation biologists and landscape ecologists includes a much more limited range of fragments – i.e. those of relatively small size. As observed in the present study, collections of small islands often fail to show a significant species–area relationship (see discussion of the 'small island effect' in Brown & Lomolino, 1998, p. 393; Lomolino, 2000a, 2000b). Within a collection of small islands, larger size should confer benefits in the form of slightly higher persistence probabilities. Such modest benefits, however, should be rendered insignificant in the face of more demonstrable variation in habitat characteristics among fragments and across the matrix.

Finally, the positive correlation between fragment area and richness of matrix species (as revealed by multiple regression analysis, Table 5) suggests at least two alternative explanations. Population densities, and therefore persistence, of these species may increase with fragment area, just as predicted by the equilibrium theory. On the other hand, these are not old-growth-dependent species. Their richness and incidences in larger fragments of old growth may simply reflect the increased total amount of edge habitat available for invasion by these species, just as forest edges in other regions facilitate invasions by cowbirds, skunks and other nest parasites and predators (e.g. see Murcia, 1995; Hawrot & Niemi, 1996; Donovan *et al.*, 1997; Woodroffe & Ginsberg, 1998). In Olympic National Forest, old-growth forest edges may constitute a distinct and important habitat for Townsend chipmunks, mule deer and other matrix species. Put another way, the area-*per se* hypothesis (*sensu* equilibrium theory; MacArthur & Wilson, 1967) and habitat diversity hypothesis are not mutually exclusive. As fragment size increases, the total area of each type of habitat (edge or otherwise) increases, thus increasing carrying capacity for a greater diversity of species — both generalists and specialists.

CONCLUSION

Our studies have identified some important and potentially fruitful topics for future research. First, we echo the calls of others for increased attention to the ecological significance of the habitat matrix (e.g. Harris, 1984; Brown & McDonald, 1995; Laurance & Bierregaard, 1997; Tilman & Kareiva, 1997; Wiens, 1997). Unlike their oceanic counterparts, intervening landscapes are unlikely to be homogeneous for archipelagos of habitat islands. In this study, species richness and species composition of mammals was strongly associated with coverage of old growth and stands of relatively old second-growth forests in the adjacent matrix. Our other studies in this region also revealed that mammalian community structure was strongly influenced by the proximity of a site to continuous old-growth forests and corridors (Songer *et al.*, 1997; Lomolino & Perault, 2000; Perault & Lomolino, 2000). There now appears to be a growing list of studies reporting the influencing of matrix characteristics and what we term landscape impedance on the structure of isolated communities, e.g. hazel grouse (*Bonasa bonasia*) across forested and agricultural landscapes (Aberg *et al.*, 1995); tree frogs (*Hyla arborea*) in a fragmented forest landscape (Vos & Stumpel, 1995); small mammals of isolated, montane forests in the American South-west (Lomolino *et al.*, 1989; Lomolino & Davis, 1997); and small mammals of forested, nearshore islands of freshwater and coastal archipelagos of the Great Lakes Region, USA (Lomolino, 1994).

Secondly, our results support the calls for additional studies of the influence of edge habitats

on invasions by non-target (i.e. matrix) species (see discussion of edge effects in Laurance & Bierregaard, 1997, pp. 29–84). For example, edge habitats appear to facilitate invasion by common deer mice, Townsend chipmunks and spotted skunks, which probably compete with or prey upon old-growth dependent species.

Thirdly, in addition to the potential importance of interactions among species, our results suggest that richness within fragments may also be influenced by the interactive effects of independent variables (area, isolation and habitat conditions). In their study of small mammals inhabiting rain forests of New South Wales, Australia, Dunston & Fox (1996) also reported significant, interactive effects, with species richness varying more with habitat [level of disturbance, *sensu* Dunston & Fox (1996)] for the smaller and less-isolated fragments. It is likely that such interactive effects are not unique to these systems and, if so, then studies that consider the potential importance of interactions among species and among independent variables should provide clearer and more comprehensive understanding of the forces structuring fragmented communities (see also Fox & Fox, 2000).

Fourthly, the tendency for species–area relationships to be weak or non-significant for collections of small isolates is another phenomenon that merits more attention. How general is the 'small island' effect for archipelagos of fragmented habitats? Can we estimate the critical range in fragment area, beyond which species richness increases with area in a manner consistent with predictions based on conventional island biogeography theory? Equally important, we can ask whether this critical range varies in any logical fashion among species groups or among types of ecosystems (e.g. greater critical range for large vs. small species, for carnivores vs. herbivores, or for ecosystems with relatively high vs. low levels of disturbance)?

Finally, we call for additional studies on differential responses among species. Even within a narrowly defined functional group, such as old-growth dependent mammals, component species often differ significantly in characteristics influencing their abilities to colonize and maintain populations in old-growth fragments. Do these characteristics covary in any systematic way? For example, do good immigrators and colonists also tend to require fragments with higher carrying capacities? On first principles, we predict that communities of bats and birds would be less influenced by isolation and landscape impedance than would the non-volant mammals we studied. On the other hand, populations and communities of amphibians, which are presumably more limited in their abilities to disperse across the relatively xeric clearcuts, should exhibit an even higher sensitivity to conditions of the surrounding landscape. While these may seem to be logical predictions of certain relevance to conservation biologists, there is unfortunately a great paucity of rigorous studies addressing these questions. We firmly believe, however, that the necessary data may be available, or may readily be collected. Such studies should provide important empirical and conceptual advances for conserving biological diversity of fragmented ecosystems.

ACKNOWLEDGMENTS

REFERENCES

Aberg, J., Jansson, G., Swenson, J.E. & Angelstam, P. (1995) The effect of the matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. *Oecologia*, **103**, 265–269.

Brown, J.H. & Lomolinom, M.V. (1998) *Biogeography*, 2nd edn, p. 692. Sinauer Associates, Sunderland, MA.

Brown, J.H. & McDonald, W. (1995) Livestock grazing and conservation on southwestern rangelands. *Conservation Biology*, **9**, 1644–1647.

Brubaker, L.B. (1991) *Climate change and the origin of old-growth Douglas-fir forests in Puget Sound lowland. Wildlife and vegetation of unmanaged Douglas-Fir forests*. USDA Forest Service, General Technical Report PNW-GTR-285, pp. 17–24. Pacific Northwest Research Station, Portland.

Carey, A.B. & Johnson, M.L. (1995) Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications*, **5**, 336–352.

Doak, D.F. & Mills, L.S. (1994) A useful role for theory in conservation. *Ecology*, **75**, 615–626.

Donovan, T.M., Jones, P.W., Annand, E.M. & Thompson, F.R. (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology*, **78**, 2064–2075.

Dunston, C.E. & Fox, B.J. (1996) The effects of fragmentation and disturbance of rain forests on ground-dwelling small mammals on the Robertson Plateau, New South Wales, Australia. *Journal of Biogeography*, **23**, 187–201.

Environmental Systems Research Institute. (1997) *ARC/INFO. Revision 7.1*. Environmental Systems Research Institute, Inc., Redlands, CA.

Fox, B.J. & Fox, M.D. (2000) Factors determining mammals species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecology and Biogeography*, **9**, 19–38.

Harris, L.D. (1984) *The fragmented forest: island biogeography theory and the preservation of biotic diversity*, p. 211. University of Chicago Press, Chicago.

Hawrot, R.Y. & Niemi, G.J. (1996) Effects of edge-type and patch shape on avian communities in a mixed conifer–hardwood forest. *The Auk*, **113**, 586–599.

Holmes, B. (1996) Life on the edge. *New Scientist*, **151**, 38–40.

Laurance, W.F. & Bierregaard, R.O. Jr, eds (1997) *Tropical remnants: ecology, management, and conservation of fragmented communities*, p. 616. University of Chicago Press, Chicago.

Larrison, E.J. & Fisher, A.C. (1976) *Mammals of the northwest: Washington, Oregon, Idaho and British Columbia*, p. 256. Seattle Audubon Society, Seattle, Washington.

Lomolino, M.V. (1986) Mammalian community structure on islands: immigration, extinction and interactive effects. *Biological Journal of the Linnaean Society*, **28**, 1–21.

Lomolino, M.V. (1994) Species richness patterns of mammals inhabiting nearshore islands: area, isolation and immigration filters. *Journal of Mammalogy*, **75**, 39–49.

Lomolino, M.V. (2000a) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**, 17–26.

Lomolino, M.V. (2000b) A species-based theory of insular zoogeography. *Global Ecology and Biogeography*, **9**, 39–58.

Lomolino, M.V. & Channell, R. (1995) Splendid isolation: patterns of geographic range collapse in endangered mammals. *Journal of Mammalogy*, **76**, 335–347.

Lomolino, M.V. & Davis, R. (1997) Biogeographic scale and biodiversity of mountain forest mammals of western North America. *Global Ecology and Biogeography Letters*, **6**, 57–76.

Lomolino, M.V. & Perault, D.R. (2000) Assembly and dis-assembly of mammal communities in a fragmented temperate rain forest. *Ecology*, **81**, 1517–1532.

Lomolino, M.V., Brown, J.H. & Davis, R. (1989) Island biogeography of montane forest mammals in the American Southwest. *Ecology*, **70**, 180–194.

MacArthur, R.H. & Wilson, E. (1967) *The Equilibrium theory of Island Biogeography*, p. 203. Princeton University Press, New Jersey.

Murcia, C. (1995) Edge effects of fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58–62.

Norse, E.A. (1990) *Ancient forests of the Pacific Northwest*, p. 329. Island Press, Washington DC.

Old-growth Definition Task Group (Franklin, J.F., Hall, F., Laudenslayer, W., Maser, C., Nunan, J., Poppino, J., Ralph, C.J. & Spies, T.) (1986) *Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California*, p. 7. USDA Forest Service, Pacific Northwest Research Station Note PNW-447. Portland, Oregon.

Perault, D.R. (1998) Landscape heterogeneity and the role of corridors in determining the spatial structure of insular mammal populations. PhD Dissertation. University of Oklahoma, Norman, Oklahoma.

Perault, D.R. & Lomolino, M.V. (2000) Corridors and mammal community structure across a fragmented, old-growth forest landscape. *Ecological Monographs*, in press.

Peterson, D.L., Schreiner, E.G. & Buckingham, N.M. (1997) Gradients, vegetation and climate: spatial and temporal dynamics in the Olympic Mountains, U.S.A. *Global Ecology and Biogeography Letters*, **6**, 7–17.

Rosenberg, K.V. & Raphael, M.G. (1990) Effects of fragmentation on vertebrates in Douglas-fir forests. *Modeling habitat relationships of terrestrial vertebrates* (ed. by J. Verner, M.L. Morrison & C.T. Ralph), pp. 263–272. University of Wisconsin press, Madison, WI.

Shafer, C.L. (1990) *Nature reserves: island theory and conservation practice*, p. 189. Smithsonian Institution Press, Washington.

Songer, M.A., Lomolino, M.V. & Perault, D.R. (1997) Habitat selection and niche dynamics of deermice (*Peromyscus oreas* and *P. maniculatis*) in a fragmented, old-growth forest landscape. *Journal of Mammalogy*, **78**, 1027–1039.

SYSTAT Inc. (1997) *SYSTAT for windows: statistics*, Version 7.0 Edition. SYSTAT Inc., Evanston, Illinois.

Tilman, D. & Kareiva, P. (1997) Spatial ecology: the role of the space in population dynamics and interspecific interactions, p. 368. *Monographs in population biology*, number 30. Princeton University Press, New Jersey.

Vos, C.C. & Stumpel, A.H.P. (1995) Comparison of habitat–isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). *Landscape Ecology*, **11**, 203–214.

Wardle, D.A. & Zackrisson, O. (1997) The influence of island area on ecosystem properties. *Science*, **277**, 1296–1300.

Whitlock, C. (1992) Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. *Northwest Environment Journal*, **8**, 5–28.

Wiens, J.A. (1997) Metapopulation dynamics and landscape ecology. *Metapopulation biology* (ed. by I. Hanski & M. Gilpin), pp. 43–62. Academic Press, San Diego.

Wilson, D.E. & Reeder, D.M., eds (1993) *Mammal species of the world*, p. 1206. Smithsonian Institution Press, Washington, DC.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2129.