AN ABSTRACT OF THE THESIS OF

Keith A. Swindle for the degree of Master of Science in Wildlife Science presented on October 16, 1997. Title: Landscape Composition Around Northern Spotted Owl Nests, Central Cascade Mountains, Oregon.

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This study describes the composition of forest landscapes surrounding northern spotted owl (*Strix occidentalis caurina*) nests in the central Cascade Mountains of Oregon. I compared forest composition around 126 owl nests in 70 pair territories with forest composition around 119 points drawn randomly from all terrestrial cover-types, and around 104 points drawn randomly from the old-forest (closed canopy, > 80 yrs) cover type. All nest sites and random points were drawn from U.S. Forest Service lands and were not drawn from privately owned lands or Wilderness Areas.

Forest cover was classified on a Landsat Thematic Mapper image. I quantified the percentage of old-forest within 200 concentric circular plots (0.04-5.0-km radii), centered on each analyzed point, using a geographic information system. I used logistic regression to make spatially-explicit inferences.

Owl nests were surrounded by more old-forest when compared to points drawn randomly from all terrestrial cover types: there was significantly ($P < 0.05$) more old-forest around the owl nests in plots as large as 1.79 km in radius. When compared to points drawn randomly from the old-forest cover type, owl nests were

surrounded by significantly ($P < 0.05$) more old-forest in plots with 0.17-0.80-km radii.

Exploratory analyses suggest that the landscape scales most pertinent to northern spotted owl nest site positioning in this study area appear to be (in descending order): the surrounding 10-15 ha (≈200-m radius), the surrounding 25-30 ha (≈300-m radius), the surrounding 200 ha (800-m radius), and possibly the surrounding 700 ha (1,500-m radius).

This study supports the assertion that northern spotted owls are strongly associated with older forests. The results also indicate that owl nests are most associated with higher proportions of old-forest near the nest implying that the arrangement of habitat is important for nest-site selection/positioning. Since spotted owls in the central Cascade Mountains of Oregon are known to have home-ranges that average 1,769 ha, it is important to recognize that these results apply to nest-site selection/positioning on the landscape and not to the amount of habitat necessary for pair persistence or successful reproduction.

Landscape Composition Around Northern Spotted Owl Nests, Central Cascade Mountains, Oregon

by

Keith A. Swindle

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Keith A. Swindle, Author

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I have often wondered what this nation would look like without the efforts of those whom have cared about and for its natural heritage. Having had the honor and pleasure to know and work with the following individuals and organizations I now know what the nation would look like without their stewardship and citizenship. All too often those of us concerned about our cultural heritage forget that it is inextricable from our natural heritage. I know that the following people and organizations have served the people of this nation for years to come through their love for and dedication to our natural resources and their stewardship. In their regard, I put forward this document, knowing that it cannot serve justice to their efforts that are, however, realized on the landscape. I do hope that this study will provide some further assistance to understanding the northern spotted owl; a fascinating and remarkable component of the world we belong to that would be inexcusable and unforgivable to lose.

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INTRODUCTION

Numerous habitat association studies have addressed the question: Are northern spotted owls (*Strix occidentalis caurina*) associated with old forests (Forsman et al. 1984; Thomas et al. 1990; Ripple et al. 1991a, 1997; Bart and Forsman 1992; Lehmkuhl et al. 1993; Hunter et al. 1995)? Researchers conducting these studies concluded, without exception, that there was a clear and strong association between owl occupancy and mature and old-growth forests (hereafter old-forests) *or* forests with structural characteristics of old-forests. The northern spotted owl was listed as a federally threatened species by the U.S. Fish and Wildlife Service (Federal Register 55 [123]: 26114-26194, 26 June 1990) and has been the focus of a national controversy because of its association with these economically valuable forests (Dixon and Juelson 1987; Salwasser 1987; Simberloff 1987; Murphy and Noon 1991, 1992). While it seems clear that the presence and amount of structurally complex forests are important to northern spotted owl occupancy, relatively little is known about how the arrangement of those forests, relative to owl nest sites, affect individual owl pairs.

Following WWII through the 1980's forest on federal lands was cut in dispersed units of 10-20 ha. (Smith 1985, Franklin and Forman 1987, Swanson and Franklin 1992). By 1990, approximately 30% of federal forest land in the Pacific Northwest had been converted to plantations (Swanson and Franklin 1992). As a result of dispersed harvest units and even-aged forest management, many of these federal forest landscapes are now mosaics of different aged forest patches. Although such fragmentation of the landscape adheres well to the long-held tenet that wildlife diversity increases with increased juxtaposition of habitats (Johnston 1947, Yahner 1988), managing for maximum edge may negatively affect interior species that are dependent on extensive stands of contiguous habitat (Harris 1984). Concern for forest-interior species (i.e. species that perform all or most of their activities away from stand edges–see Johnston 1947, Forman and Godron 1986, and Yahner 1988) has prompted consideration of alternative cutting patterns to reduce fragmentation of old-growth forests (Swanson and Franklin 1992). The northern spotted owl uses large tracts of late-successional forest (Thomas et al. 1990; Carey et al. 1990, 1992; Ripple et al. 1991a; USDI 1992; Bart and Forsman 1992; Johnson 1993), bases its activities centrally around one or more nests (Forsman et al. 1984) typically located in a "core-area" or activity center, and is generally considered a forest-interior species. The assumption, that spotted owls rely on centrally located, contiguous core-areas, has been used for management recommendations and commonly implemented by several land management agencies. However, the spatial scales at which spotted owls are "interior" species and how forest fragmentation affects them (beyond the direct loss of old-forest habitat) remain unclear, especially regarding parameters of fitness (survival rates and reproductive performance–Noon and Biles 1990, Murphy and Noon 1992).

Fragmentation of a species' preferred habitat has two interrelated effects: direct loss of that habitat, and change in the quality of the remaining habitat due to its resulting arrangement and juxtaposition. It is difficult to tease these effects apart. For example, if spotted owls are associated with older forests, and some percentage of those forests are harvested, then an obvious conclusion is that spotted owls will be negatively impacted due to a direct loss of habitat. However, the pattern of the harvest might impact the owl synergistically for a variety of reasons (e.g., increased travel distances for foraging, changes in microclimate [Chen et al. 1990], improved conditions for competitors [Hamer et al. 1989] and/or predators [Johnson 1993], etc.). These impacts are likely to be dependent upon scale (especially for species with large home-ranges), which further complicates the issue. So, an understanding of the landscape scales that owls recognize for nest-site positioning may be helpful before the effects of fragmentation on fitness parameters can be understood.

Because owls tend to base their activities centrally, require large amounts of old-forest habitat, and seem to use space according to optimal foraging theory (Carey and Peeler, 1995), I predicted that reproductively active owl pairs positioned themselves on the landscape so as to maximize the amount of old-forest available. In other words, both the amount and the spatial position of habitat relative to the nest-site were likely to be important. Thus, if arrangement of habitat was important to owls it should be more important closer to the nest, therefore I hypothesized that owls selected landscapes where the proportion of old-forest habitat was centrally weighted or "clumped" in its general arrangement. This prediction was supported by other studies where owls consistently positioned their nest-sites in forest patches that were larger on average than was available on those landscapes (Ripple et al. 1997, Perkins et al., in review), however, the study areas of Ripple et al. (1997) and Perkins et al. (in review) were more fragmented than my study area. The simple measure of patch size can quantify how nest sites were placed with respect to interior habitat. However, the contiguity of my study area (i.e., the matrix is still old-forest and the patches are non-forest or young plantations) renders this measure relatively useless. A second measure, distance to edge, has been instructive in other studies (Johnson 1993) where aerial photo interpretation was used. However, applying this measure to satellite imagery is problematic because of its extremely high spatial resolution (i.e. individual pixels may be considered patches) which calls for an arbitrary definition of a minimum patch size. Additionally, owls are restricted by their need for a suitable nest cavity or structure which may not be ideally positioned with respect to edge but may still be selected (over other suitable nest structures) because of its position relative to the amount of surrounding old-forest (i.e. more optimally located with respect to preferred habitat). For these reasons I did not use traditional landscape metrics to address this question. Rather than develop new landscape metrics to deal with these problems, I applied analysis methods that allowed scale-specific spatial inferences in spite of using scale-independent measures of habitat. Additionally, I framed the hypothesis differently than previous studies by restricting (stratifying) my inquiry to the habitat of interest (i.e., selected random points from *within* old-forest habitat).

There were two main goals of this study. First, I replicated portions of the studies of Ripple et al. (1991a, 1997), Lehmkuhl et al. (1993), Hunter et al. (1995), Meyer et al. (in review), and Perkins et al. (in review), by addressing the question: Are northern spotted owls associated with mature and old-growth forests? My study had a larger sample size than those studies and differed in general location from all of those studies except Ripple et al. (1991a). In comparison to Ripple et al. (1991a) this study differed by having refined sampling and analytical techniques, a more comprehensive data set, and a slightly different study area with a satellite derived habitat classification.

Secondly, I attempted to ask the question: Assuming that owls 'select' old-forests, do they position their nests so as to maximize the amount of old-forest in the immediate vicinity? This question could not be directly addressed without a controlled, manipulative experiment. However, I asked a related question in an observational context: Is there more old-forest around northern spotted owl nests than around points randomly drawn from old-forest? To accomplish this, owl locations were compared to random locations that were restricted to old-forest. I predicted that for small plot sizes, the amount of old-forest would be similar for these two groups, but as plot sizes became larger, owl nests would have significantly more old-forest indicating an association with higher amounts or "clumps" of old-forest within a given area. Finally, as plot sizes became very large the amounts of old-forest around both sets of points would become similar again.

To address these questions, I used a combination of statistical analyses (outlined by Ramsey et al., 1994) and landscape analysis techniques that allowed scale-specific inferences regarding landscape composition for each of the questions posed by the objectives. In other words, the plot sizes or spatial scales where these differences diverged and converged would be instructive as to the landscape scales and amounts of old-forest with which nesting spotted owls were most associated.

STUDY AREA

The study was located in the central portion of the western slope of the Cascade Mountain Range of Oregon, and included portions of the Blue River, Mckenzie Bridge, and Sweet Home Ranger Districts of the Willamette National Forest as well as some interspersed private holdings (43°45'-44°30'N, 121°45'-122°30'; Fig. 1). The study area was bounded by and did not include the Three Sisters and Mt. Washington Wilderness areas on the east and by private lands and lands administered by the Bureau of Land Management on the west. Specifically, the study area was defined by the minimum convex polygon formed by adding a 3.4-km buffer (equal to the maximum plot radius used by Ripple et al. 1991a) to the outermost spotted owl activity centers. Topography was typical of the Western Cascades Province (Franklin and Dyrness 1973), with mountainous terrain deeply dissected by rivers and streams. Elevations ranged from 400 to 1500 m. The climate was maritime with wet, mild winters and dry, warm summers. Climatological data collected at the primary meteorological station (elevation 426 m) in the H. J. Andrews Experimental forest (the center of the study area) during the period of 1973-1984 yielded a mean annual temperature of 8.5 C with monthly ranges from 0.6 C in January to 17.8 C in July (Greenland 1994). Average annual precipitation was 2,302 mm 71% of which fell from November through March. Mean annual precipitation was greater at higher elevations (e.g., 2,785 mm at 1,203 m)and was often in the form of snow in the winter months with snow packs forming above 1,050 m and persisting into June in some years (Bierlmaier and McKee 1989, Greenland 1994).

The study area was located within the Western Hemlock (*Tsuga heterophylla*) Zone, the most extensive vegetation zone in western Oregon (Munger 1930, Franklin

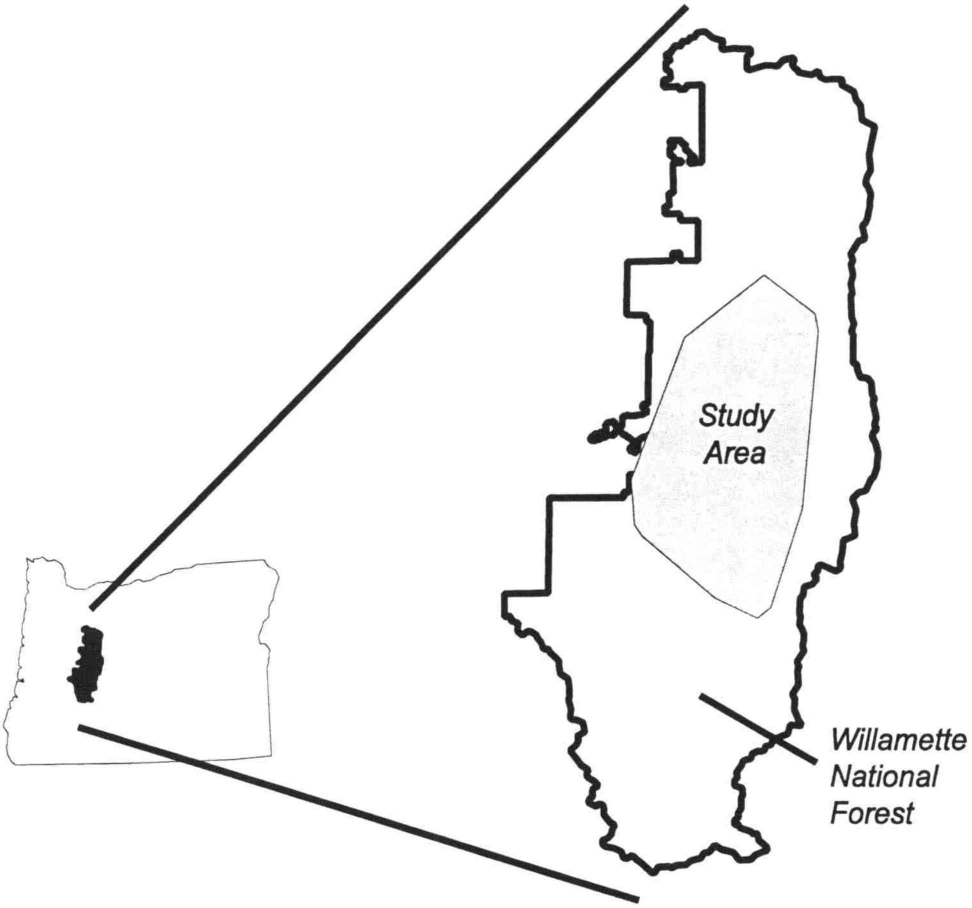

Figure 1. Map of study area in the Willamette National Forest, Oregon.

and Dyrness 1973), dominated by sub-climax forests of Douglas-fir (*Psuedotsuga menziesii*), western hemlock, and western red-cedar (*Thuja plicata*). Although 49% of the area has been converted to young conifer plantations through timber harvest or is otherwise not suitable as spotted owl nesting habitat, the remainder is comprised of older forests (reanalysis of study area portion of satellite image provided by Cohen et al., 1995).

Very little harvest took place in this study area until after WWII and the majority of harvests that have taken place since that time have been regeneration or clear-cut harvests (Ripple et al. 1991b). Consequently, the remaining forests were easily classified because they tended to be either < 40 years of age (poor habitat for spotted owls) or >200 years (excellent habitat for spotted owls). The dichotomous character of habitat in this area offered an excellent opportunity to examine the effects of habitat arrangement on spotted owl nest-site selection.

METHODS

Habitat Classification

Cohen et al. (1995) defined and mapped 12 land-cover classes based on a 1988 Landsat Thematic Mapper image that encompassed the entire study area (Table 1). Pixel resolution of the image was 25 x 25 m and overall accuracy was 82% (individual class accuracy was 56-100%; as determined from ground truthing by Cohen et al. 1995). Using the geographic information system (GIS) ERDAS (1990) I reclassified the image by lumping the 12 existing classes into four habitats that were biologically relevant to spotted owls (Table 1). This increased overall accuracy to 93% (88-100% for individual classes) because most of the error in the imagery was in the younger age-classes (Cohen et al. 1995).

Class 1 (water) of Cohen et al. (1995) was retained, as large bodies of water provided useful reference points. Classes 2-8 (non-closed-canopy forest) were considered to be habitats not capable of supporting spotted owl roosting, foraging, or nesting activities. These classes were lumped into a single class called "non-habitat". Classes nine and ten (closed-canopy forests < 80 yrs.) were lumped into a class called "young forest"; the only difference between these classes was the presence of hardwoods, which was probably not biologically relevant to owls in the central Cascade Mountains of Oregon. Classes 11 and 12, representing mature (80-200-year old) and old-growth (>200 year-old) forests respectively, were combined into a single class called "old-forest". This combination was justified for several reasons. First, mature and old-growth classes are difficult to distinguish using remote sensing techniques (Fiorella and Ripple 1993) and consequently 29.4% of the observations of these classes on the original image were mis-classified (Cohen et al. 1995). However,

Table 1. Cover-type re-classification of 1988 Landsat Thematic Mapper image (originally classified by Cohen et al. 1995) of the central Cascade mountains, Oregon.

Class	Cover Type	Re-classification	Cover Type
1	Water	1	Water
2	Snow/Ice	2	Non-Habitat
3	Lava/Rock	2	Non-Habitat
4	Agriculture/Nonforest - open	2	Non-Habitat
5	Agriculture/Nonforest - semi-open	2	Non-Habitat
6	Agriculture/Nonforest - closed	2	Non-Habitat
7	Hardwood/Conifer Forest - open	2	Non-Habitat
8	Hardwood/Conifer Forest - semi-open	2	Non-Habitat
9	Hardwood/Conifer Forest - closed	3	Young
10	Closed Conifer Forest - young	3	Young
11	Closed Conifer Forest - mature (80-200 years)	4	Old-forest
12	Closed Conifer Forest - old (200+ years)	4	Old-forest

when distinguishing mature closed-conifer from young closed-conifer or old closed-conifer from young closed-conifer the error rates were much lower (12% for mature vs. young, 0% for old vs. young; Cohen et al. 1995). Second, telemetry of northern spotted owls within this study area indicated that mature forests were used as expected or more than expected while younger forests were used less than expected (Miller and Meslow 1989). Third, the assumption that mature forests contribute as northern spotted owl habitat is supported by researchers in other portions of the species range

(Thomas et al. 1990) and consequently makes this data set more comparable to other studies (e.g., Ripple et al. 1991a, 1997; Hunter et al. 1995).

After re-classifying the image I noted that the high resolution (25 x 25 m) seemed to cause an underestimate of the amount of old-forest on the landscape when compared to Ripple et al. (1991a) who used aerial photo interpretation to estimate old-forest amounts in the same vicinity. One structural characteristic of old-growth was a very heterogeneous canopy. With high resolution Thematic Mapper data these canopy gaps were apparently classified as cover-types other than old-forest. Functionally, for northern spotted owls these within-stand gaps serve as old-forest habitat. Consequently, estimates of old-forest derived from a sum of all old-forest classified pixels was probably biased low in the Thematic Mapper data. Conversely, individual or small groups of old-forest trees isolated in a clear-cut or other non-habitat patch, were counted as habitat when functionally, they did not contribute as habitat. Visual assessment of the image indicated that isolated old-forest pixels in non-habitat patches were much less common than isolated non-habitat pixels in old-forest patches. To partially correct for this problem, I smoothed the image by performing a 2-pixel radius, moving circular-window, majority SCAN procedure (ERDAS 1990). This effectively removed all patches < 0.4 ha in size.

Approximately 50% of the landscape was classified as old-forest, 30% as non-habitat, and 20% as young forest (Table 2). Smoothing the image resulted in an increase of old-forest by nearly 3% at the expense of a reduction in slightly more than 2% and < 1% in young forest and non-habitat, respectively (Table 2).

Table 2. Percentages of the study area in each cover type and results of a 2-radius, majority-SCAN, smoothing procedure (ERDAS 1990) on a 1988 Landsat Thematic Mapper image of the central Cascade mountains, Oregon.

Cover Type	Description	Unsmoothed	Smoothed
1	Water	0.35	0.37
2	Non-Habitat	30.26	29.69
3	Young	21.44	19.09
4	Old-forest	47.95	50.84

Lastly, I discovered and corrected a mis-registration error on the image which was independently discovered and quantified after initial release of the image (John Gray and Maria Fiorella, personal communication). The error was caused by assignment of an incorrect horizontal datum during the original geocoding of the image and resulted in an offset error of -96 m in the x-direction and -23 m in the y-direction (John Gray, personal communication). I corrected the image by reassigning (adding 96 m and 23 m in x- and y-directions respectively) the original projection. Neither the error nor the correction influenced the habitat classification accuracy of the image. However, if left uncorrected, all owl nests would have been plotted 96 m and 23 m too far to the east and north respectively.

Owl Activity Centers

One hundred and one northern spotted owl territories were surveyed for occupancy for ≥ 4 years from 1987 through 1995 as part of an ongoing study (see Miller et al. 1996). Within each territory the best owl locations were identified as activity centers. Owl activity centers were ranked in descending order as follows: nest trees, locations of recently fledged juveniles, and day roosts. A total of 167 activity centers were identified for the 101 territories. Of these, 143 nest trees were located in 77 territories, 10 locations of fledged juveniles for 10 territories, and 14 day roosts in 14 territories. Each of the 14 day roosts was the actual day roost nearest the geographic center point among all day roosts identified for that territory. I obtained Universal Transverse Mercator locations[1] for 126 (of the 143 known) nest trees, (representing 70 territories) using a Geographic Positioning System (GPS; Model PRO XL with TDC2 data logger, Trimble 1996) with differential correction (DGPS; using Pfinder software, Trimble 1996).

Using the UTM coordinates, I then located the pixel containing each identified point on the classified GIS image. Of the 126 DGPS located nest trees, 101 (80%) fell in pixels classified as old-forest on the unsmoothed image. I was confident that the most of the remaining 25 activity centers (not classified as old-forest) were errors, because all points were identified in the field and rarely occurred[2] (≤ 5%) in young forest.

I identified two potential sources of error: mis-classification of habitat, and mis-registration. Mis-classification error represents instances when a point was

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[1] This GPS unit is reportedly capable of sub-meter accuracy. My field tests (25 trials of a single known point) indicated the unit always registered within 1.7 m of a known point.

[2] Northern spotted owls will use forests < 80 years of age particularly when residual or "legacy" structural characteristics exist (or where coastal redwood [*Sequoia sempervirens*] forests occur; Thomas et al. 1990, USDI 1992). However, such behavior is uncommon in this study area because these habitats are rare for several reasons. First, the absolute amount of closed-canopy forest < 80 years of age is small (< 20% of study area), and most of this is quite young (< 30 years) and essentially unsuitable as spotted owl habitat. Second, very few stands < 80 years of age have substantial residual structural components due to the pre-dominance of clear-cutting in this area (Ripple et al. 1991b, Swanson and Franklin 1992, Spies et al. 1994, personal observation).

accurately placed on the image but the habitat was mis-identified (i.e., differed from field assessment) or was classified as non-old-forest due to the interaction of high image resolution and old-growth canopy heterogeneity discussed previously. Mis-registration occurred if the point was not accurately placed on the image, and could be due to either or both of the following reasons: 1) inaccuracy of original location of the tree, and 2) error in registration between orthophoto-quad and GIS image. Because I used DGPS to locate the trees and corrected the known registration error in the image, significant mis-registration errors seemed unlikely.

After smoothing the image, 19 of these 25 points fell in old-forest, however, five (4%) of the nests originally classified as old-forest were changed to non-old-forest. It is likely that these five nests were either near an edge or were in isolated old-growth trees surrounded by other habitats. Thus, the net result after smoothing was 113 (90%) of the owl nests fell in pixels classified as old-forest.

Of the eight remaining points, three (2%) were located in young forest pixels, and five (4%) were in non-habitat pixels. All three of the trees located in young forest were old-growth trees ≥48" dbh. Similarly, all five trees located in non-habitat pixels were old-growth ≥40" dbh. Field assessment revealed that four of them were either in or adjacent to rock outcrops, talus, or quarry, and one was near the edge of a stand of sapling trees.

In summary, on the smoothed image 113 (90%) of the 126 owl nests were located in pixels classified as old-forest, seven (6%) were located in young forest, and six (5%) were in pixels classified as non-habitat.

Random Point Selection

Two sets of random points were drawn from the study area (Fig. 2). First, a sample of 119 points (pixels) were randomly chosen (with replacement) from the classified image of the study area. Points falling on land designated as Wilderness, non-U.S. Forest Service (USFS) ownership, or areas classified as not being capable of supporting forest vegetation (e.g., open bodies of water, lava flows) were rejected (not analyzed).

A second independent set of 104 points was drawn from the image in an identical fashion to the set described above, with the additional condition that points were restricted to the old-forest cover class. The restriction of this set to old-forest allowed inference regarding selection of habitat arrangement or configuration as opposed to selection of habitat class (assuming that spotted owls selected old-forest).

Habitat Analysis

Two hundred concentric, non-overlapping, circular ring-plots were generated and overlaid on each of the 167 owl activity centers, 119 totally random points, and 104 stratified random points (hereafter referred to as old-forest random points) using the SEARCH and SUMMARY procedures in ERDAS. Each of the 200 ring-plots averaged one pixel (25m) in width and the percentage of each cover class was analyzed around each point out to a 5-km radius. The percentage of each cover-class was calculated in two ways: 1) in each of the 200 non-overlapping rings, and 2) in each of the 200 inclusive circles. The 167 owl activity centers were summarized to 101 territories by obtaining the averages for those sites with > 1 activity center (i.e. pairs that used 2 or more nest trees within the same territory). The values for a subset of 70

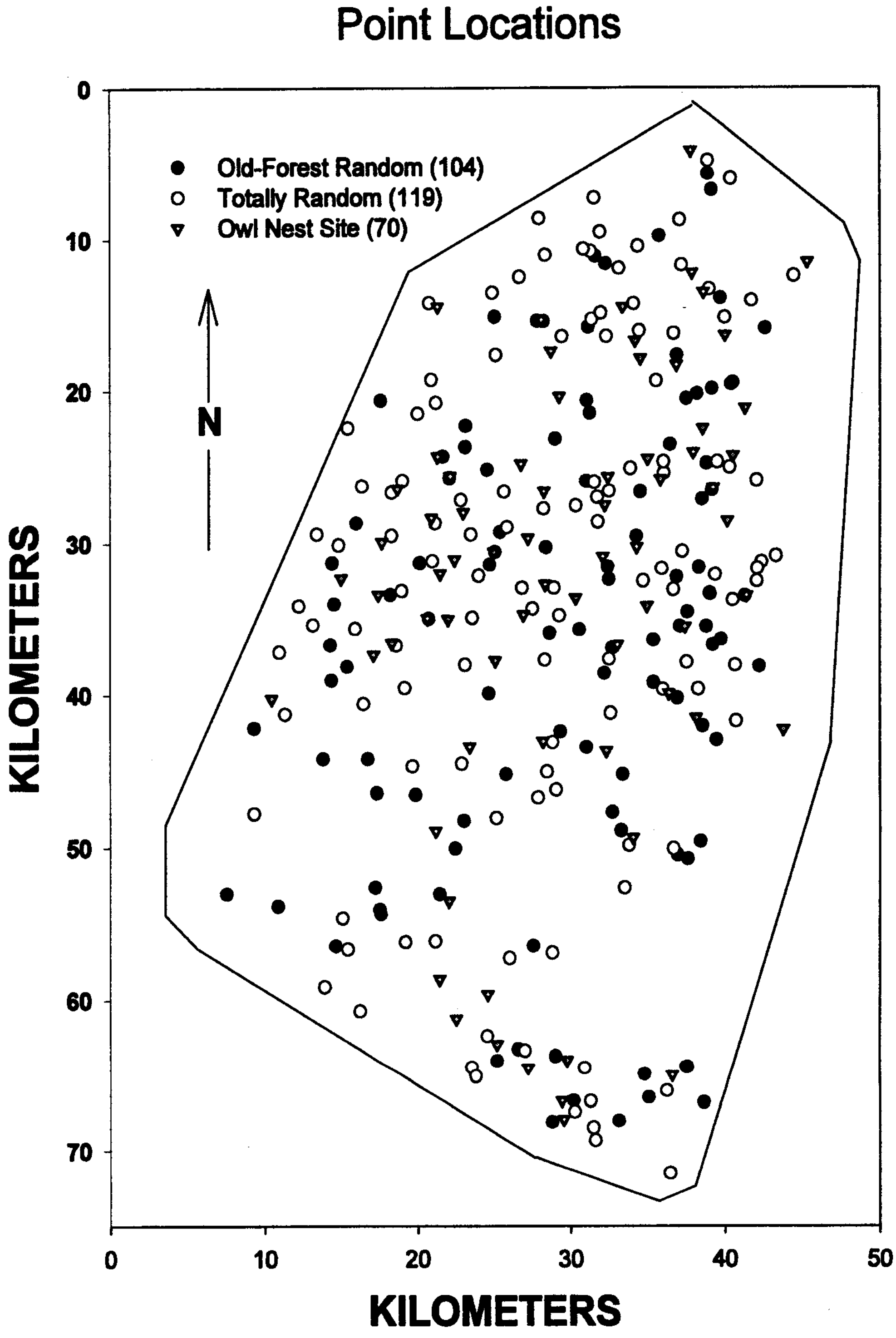

Figure 2. Locations of owl nest sites and random points in the study area. Closed circles represent points drawn randomly from the old-forest cover type, open circles represent points drawn randomly from all terrestrial cover types, and dark triangles represent owl nest sites located in the central Cascade mountains, Oregon (1987-1995).

of the 101 territories represent summaries for areas surrounding the 126 GPS-located-nest trees and will be referred to as nest sites (Fig. 2). To be more consistent with Ripple et al. (1991a) most comparisons were drawn between these 70 nest sites and the two respective sets of random points.

Statistical Design and Analyses

This was an observational "case-control" study making binary comparisons between landscapes around three sets of points: [a] owl nests versus [b] totally random points, and [a] owl nests versus [c] old-forest random points. Each set of points was defined by its level of response. For example, the points representing owl nests were selected[3] by owls (response level = 1 or yes) whereas, the points in each random set were representative[4] of points not selected by owls (response level = 0 or no). The sampling design was a retrospective product binomial scheme (Ramsey and Schafer 1997). Retrospective, as used here, referred to the sampling technique (not the theoretical approach) and indicated that sampling was carried out for each level of the response variable [for description, advantages, and limitations of retrospective sampling see Ramsey et al. 1994]. It was binomial because for each comparison, each point fell into one of two categories (i.e., owl nest site vs. random; Ramsey and Schafer, 1997). In statistical terminology, product binomial indicated that there was more than one binomial population with independent samples taken in each (Ramsey

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[3] The term "selected" is used loosely here. I agree with Ramsey et al. (1994) that terms like selection and preference are misleading for observational habitat studies because inferences from such studies are associative and not causative.

[4] Random points were drawn to be representative of the landscape. Therefore it is possible that one or more random points coincided with one or more nest-sites. Nevertheless, the case-control framework treats them as not selected.

and Schafer, 1997). I specified the sample totals obtained in each group and ensured that they were as large as some minimum based on an a priori minimum sample size formula (Ramsey and Schafer 1997, p. 669). This was analogous to an a priori determination of statistical power though the approach was confidence interval driven (see Ramsey and Schafer 1997, p.677-678).

I used logistic regression to compare landscape composition at owl nest sites versus totally random points and at owl nest sites versus old-forest random points. These methods were described and first applied in this manner by Ramsey et al. (1994) when they reanalyzed the data of Ripple et al. (1991a). Three sets of analyses compared percentages of each cover-class between the two groups at all 200 scales in [1] circles, [2] 100-m-wide rings[5], and [3] a circle of a given size plus the next larger ring (Fig. 3). Those models were expressed as:

[1] $\text{Logit}_{(\text{nest})} = \beta_o + \beta_1(\%\text{ old-forest in Circle}_x)$

[2] $\text{Logit}_{(\text{nest})} = \beta_o + \beta_2(\%\text{ old-forest in Ring}_{x+4})$

[3] $\text{Logit}_{(\text{nest})} = \beta_o + \beta_1(\%\text{ old-forest in Circle}_x) + \beta_2(\%\text{ old-forest in Ring}_{x+4})$

where, β_o = the intercept, and x = circle or ring outer radius (in pixels) 1-200.

The first set of analyses (model-set 1) was similar to those conducted by Ripple et al. (1991a, 1997), Hunter et al. (1995), Meyer et al. (in review), and Perkins et al. (in review), however, the plot sizes (spatial scales) were continuous and therefore more complete. While concentric circular plots are easily understood and can be useful for

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[5] I also used 25-m-wide (1 pixel) rings which were of interest because they were non-overlapping (more spatially independent of one another) and provided the highest resolution possible. This width gave model-sets [2] and [3] the following structures: $\beta_o + \beta_2(\%\text{ in Ring}_{x+1})$, and $\beta_o + \beta_1(\%\text{ in Circle}_x) + \beta_2(\%\text{ in Ring}_{x+1})$. The results of these tests for the old-forest class are illustrated in appendix figures A-1 through A-6.

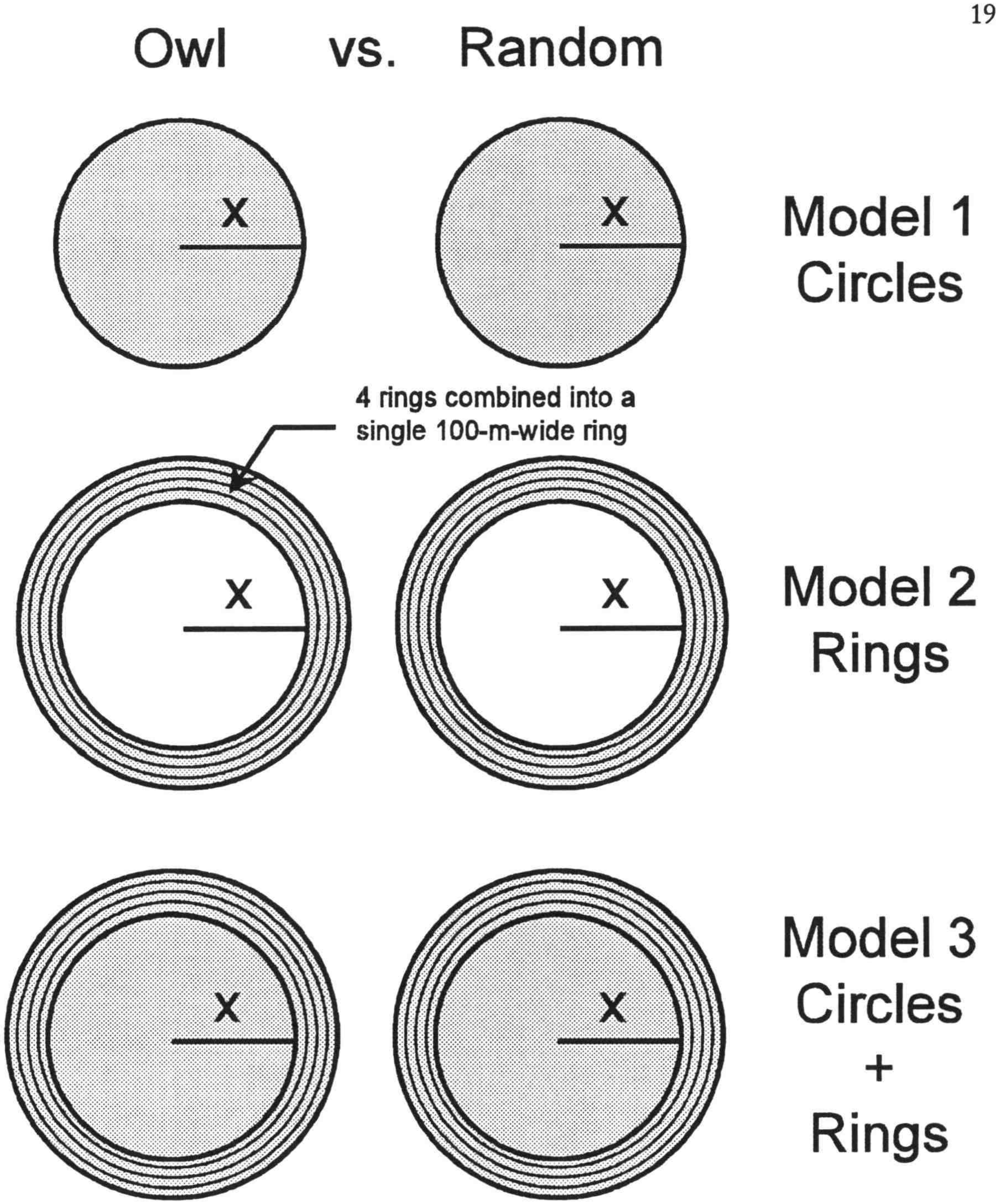

Figure 3. Illustration of habitat sampling designs and analyses. Amount of habitat in equally sized circle- and/or ring-plots around northern spotted owl nests versus random points in the central Cascade mountains, Oregon, 1987-1995 was compared. Circle-plots have an outer radius = x (where x ranges from 1 to 200 pixels that are 25 m in width) and ring-plots have an outer radius = x + 4. Note that ring-plots are four pixels (100 m) in width and the non-shaded centers of Model 2 are not analyzed.

managers, they can be mis-leading because very large circular plots may show differences in some parameter simply because there are real differences in the centers of the plots (i.e., the outer portions of the plots could be identical but because the outer portions of large circles are correlated with the inner portions they can continue to show statistical difference): such was the case with analyses conducted by Ripple et al. (1991a) who found statistically different amounts of old-forest in 3.4-km circular plots. However, Ramsey et al. (1994) demonstrated that the differences in the 3.4-km plot sizes were due to real differences in the substantially smaller plots contained within. The second set of analyses (concentric ring-plots; model-set 2), accounted for this data redundancy problem and was thus, a more spatially independent approach, and illustrated which scales contributed most to the observed differences. However, concentric rings also lack independence due to spatial autocorrelation (i.e., a pixel of a given class is more likely to be next to or surrounded by pixels of a similar class than by pixels of a different class). The third set of analyses (circle+ring; model-set 3) mathematically accounted for both of these types of correlation by treating the inner area of a plot (circle with radius = x) and the outer area of a plot (ring with radius = x + 4) as separate variables (see Ramsey et al. 1994). This provided the opportunity to identify the scales that contributed most to distinguishing owl nest-site landscapes from random landscapes and may indicate the landscape scale most important to owls for nest-site positioning purposes.

I used the three different analyses to illustrate different perspectives of these data. Using the analyses in conjunction provided a more complete exploration of the data and yielded insight as to the spatial scales that most influenced spotted owl nest-site positioning.

I chose the plot radius increment of one pixel (25 m) because it fully utilized the resolution of the Thematic Mapper data and provided the most continuous illustration of exactly where differences between proportions of old-forest around nest sites and random points occurred. I chose a ring width of 4 pixels (100 m) because it was a convenient scale of measure, was more relevant (than smaller scales) for assessment of the effects of habitat arrangement on owls, and did not mask small-scale changes in habitat composition. Analyses using other ring widths: 1, 5, 10 and 20 pixels (25, 125, 250, and 500 m, respectively) were conducted to assess the effects of ring width. Use of rings of various widths did not affect the results or conclusions but, resulted in less erratic plots (i.e., smoothed the lines in Figures 5b, 5c, 6a, 6b, 8b, 8c, 9a and 9b) for the wider rings and more erratic plots for the narrower (25-m) ring (see appendix figures A-2b, A-2c, A-3a, A-3b, A-5b, A-5c, A-6a and A-6b respectively). This process illustrated the importance of seeking patterns in the results of this multiple test methodology (i.e., where results were similar from groupings of sequentially-sized ring-plots), and reiterated the danger in drawing strong conclusions from individual ring-plot comparisons.

Model-sets 1 and 2 above were single coefficient logistic models (excluding the intercept) and were analogous to simple t-tests between two groups. I used logistic regression instead of t-tests because: it enabled me to build a more complex model (i.e., model-set 3) that allowed scale-specific (spatial) inference. Using logistic regression in this fashion is equally or perhaps more valid than using simple t-tools because it does not depend on assumptions of normality (Ramsey and Schafer 1997), and the results are expressed in terms that are intuitive (e.g., the odds that an event could have occurred given the evidence of the observed data–Ramsey et al. 1994, Ramsey and Schafer 1997). For example, a given person has some chance of contracting lung-cancer and this chance could be expressed in terms of odds: "the odds for this person to contract lung-cancer are one in a million", or they can be expressed as an odds ratio: "the odds on this horse (i.e., the ratio of the odds that this horse will lose vs. the odds that this horse will win) are two to one (2:1)". The odds for a given event to occur or to not occur, are often changed in an exponential fashion relative to (i.e., they are multiplicative of) some other co-variate. For example, a two-fold increase in the amount of a carcinogen in a room may yield a 50-fold increase in the chance that people in the room might contract cancer. In other words, the odds that they might contract cancer are greatly increased when exposed to that amount of carcinogen. Or, a jockey whose riding style irritates a champion race-horse might significantly decrease the odds that the horse will win. If irritation could be quantified we might see that a minor increase in irritation might dramatically reduce the odds of winning. In this study, I attempted to measure how changes in the amount of old-forest (in different sized circular areas around a center point) affected the odds that the center point would be associated with (or selected as a nest-site by) a pair of owls. Retrospective sampling (i.e., determining what points on the landscape owls did select [activity centers/nest sites] and then getting a measure of all points available for selection) and logistic regression, enabled me to estimate (in terms of odds) how the arrangement of old-forest habitat was associated with spotted owl nest site location.

For each model-set (1, 2, and 3) and each comparison (nest-sites vs. totally random points, and nest-sites vs. old-forest random points) two graphical displays were produced: a graph of odds and a corresponding graph of p-values. Because odds are best understood when they are expressed relative to some factor, the graphs of odds indicate how the odds that a given point was a nest-site would be changed by a 10% increase in the amount of old-forest (in each corresponding plot size)[6].

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[6] This was accomplished by exponentiating the calibrated (to represent 10%) regression coefficient (β) for each plot and then expressing it as a percentage as follows:
% change in the odds associated with a 10% increase in old-forest $= 100(e^{(10)\beta} - 1)$

Lastly, there was concern regarding the issue of multiple comparisons or compound uncertainty (Ramsey and Schafer 1997) and the resulting potential for a Type I error (a true null hypothesis [e.g., there is no difference in the amount of old-forest between the two groups] is rejected). While many statistical tools have associated procedures to adjust for compound uncertainty, I was not aware of any for this type of analysis. However, I maintain that my approach was still valid for the following reasons: 1) my interest and inference were restricted to observing trends in the data (e.g. groups of consistently small or large p-values) and not so much for specific events (e.g., erratic portions of p-value plots); 2) while 0.05 was used as a benchmark, many of the significant p-values were much smaller; and 3) inferences from this observational study were appropriately worded as associative and not causative, and strongest inferences were reserved for instances where p-values and dramatic changes in odds (which are more robust to changes in sample size and therefore more reliable) corresponded.

RESULTS

All following results and discussion apply to the old-forest class unless otherwise noted. Analyses of the classes "young forest" and "non-habitat" were conducted and are included in the appendix (Appendix figures A-7 through A-18). These classes were not of primary interest and generally are not described or discussed further. However, specific results that may affect or reflect owl biology that do not follow from discussion of the old-forest class are presented and discussed.

Owl Nest Sites vs. Totally Random Points

This compared the amount of old-forest in plots around owl nest sites and points drawn randomly from all terrestrial habitats. The following results addressed the question: "Are northern spotted owl nest-sites associated with old-forest habitat?" When considering this question a simple yes-or-no answer is of most import and scale-specific information is secondary. Consequently, only the results of the circle-plot analyses are presented and discussed in this section. In order to be consistent and comprehensive, however, the other analyses (ring-plot, and circle + ring-plot) were conducted. Readers interested as to which plot sizes were most different (with regard to the proportion of old-forest) between nest sites and random points may refer to the ring-plot and circle + ring-plot analyses presented in Appendix figures A-2 and A-3 respectively.

There was more old-forest in circular plots around spotted owl nest-sites than around points randomly drawn from the landscape in all plot sizes (Fig. 4a) and

Figure 4. Old-forest in 200 concentric circle-plots around spotted owl nest sites and totally random points. (a) percentage of old-forest[7], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of old-forest (= $100[e^{(10)\beta} - 1]$).

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[7] For illustration of graph (a), only the data from every other plot size is shown.

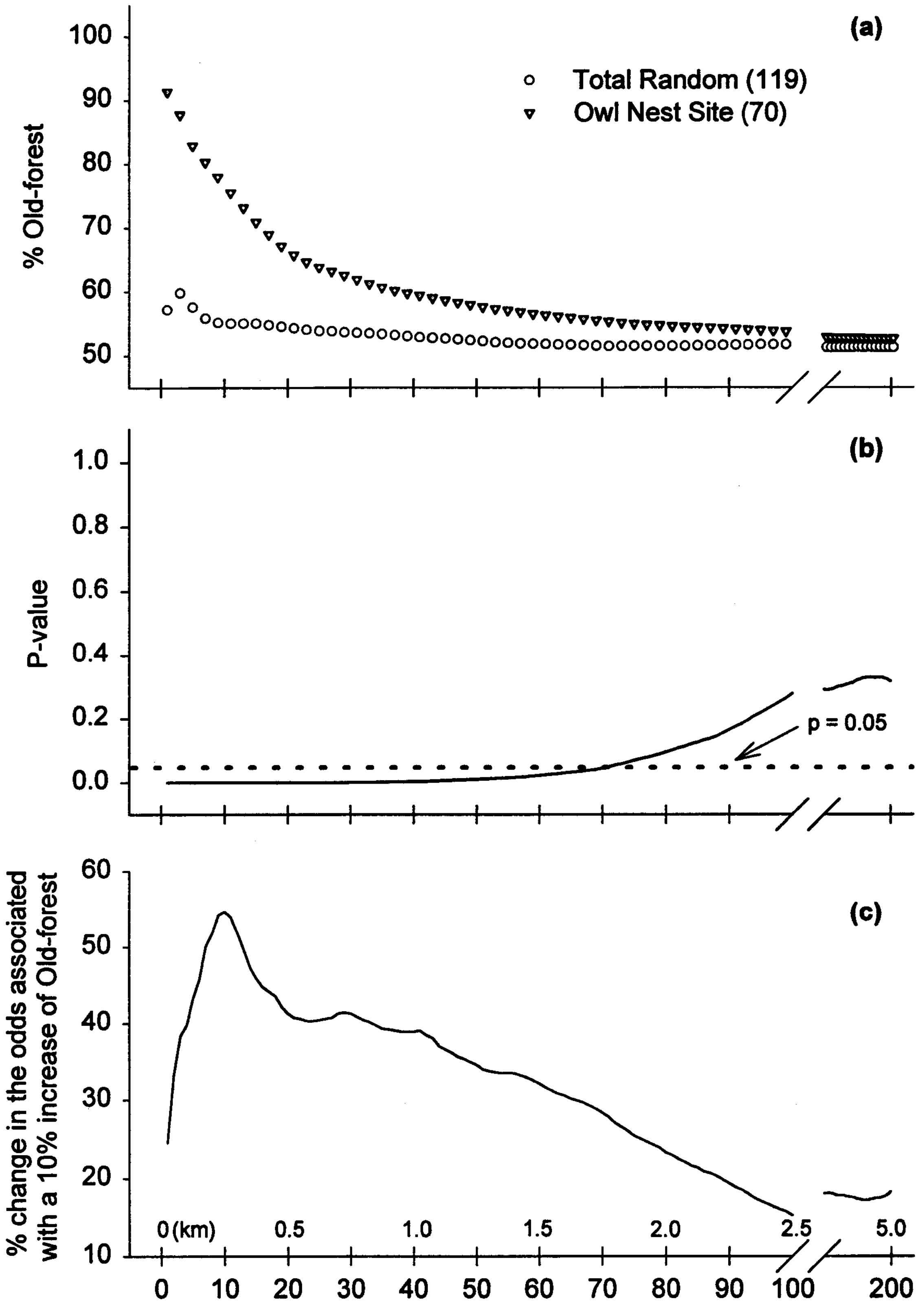
(a)
% Old-forest
100
90
80
70
60
50
○ Total Random (119)
▿ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of Old-forest
60
50
40
30
20
10
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure 4.

significantly ($P < 0.05$)[8] more in plots up to 1.79 km in radius[9] (Fig. 4b). The trend in odds ratios (which are less sensitive to changes in sample size than p-values) indicated that this difference may extend to larger plots (Fig. 4c).

Owl Nest Sites vs. Old-forest Random Points

Whereas the previous comparison used points randomly drawn from all habitat classes except water, the following results addressed the comparison of the same set of owl nest-sites versus a set of random points drawn from old-forest. This comparison asks: "Is there more old-forest around northern spotted owl nests than around points randomly drawn from old-forest?", which addresses the hypothesis that, within old-forests, owls position their nests so as to maximize the amount of old-forest in the immediate vicinity. The three sets of analyses (circle-plot, ring-plot, and circle+ring-plot) provided scale-specific information as to which plot sizes were most different (with regard to the proportion of old-forest) between nest sites and random points.

Circle-plot Analyses

There was less old-forest around owl nest sites than around points randomly drawn from old-forest in plots with radii between 0.01 km and 0.06 km and more old-forest in plots with radii between 0.06 km and 1.25 km (Fig. 5a). There was significantly ($P < 0.05$) more old-forest from 0.17 km through 0.80 km (Fig. 5b), and

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[8] I do not view the alpha level of 0.05 as a hard division between significance and non-significance, however it serves as a useful benchmark for making general interpretations especially when faced with numerous measures.

[9] Radii were approximated by total pixel area, and therefore may vary from expected, especially at small plot sizes--a result of making circular plots out of square pixels (raster data)

Figure 5. Old-forest in 200 concentric circle-plots around spotted owl nest sites and old-forest random points. (a) percentage of old-forest[10], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of old-forest ($= 100[e^{(10)\beta} - 1]$).

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[10] For illustration of graph (a), only the data from every other plot size is shown.

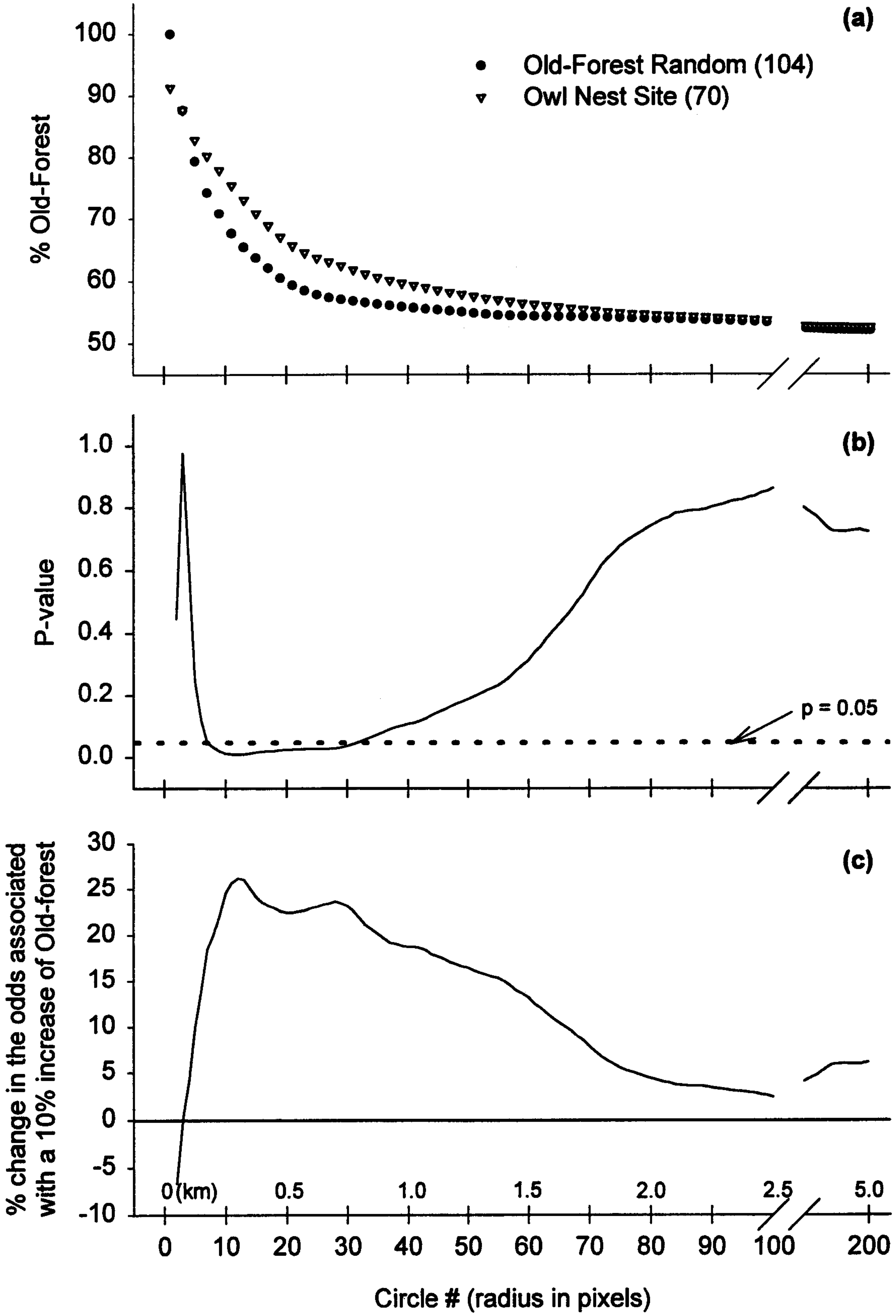
(a)
% Old-Forest
100
90
80
70
60
50
● Old-Forest Random (104)
▿ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of Old-forest
30
25
20
15
10
5
0
-5
-10
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure 5.

the trend in odds ratios indicated that this difference extended to larger scales (Fig. 5c). At scales > 2.12 km there was slightly less old-forest around owl nest sites than around old-forest random points (Fig. 5a) but these differences were not statistically significant ($P > 0.05$; Fig. 5b).

Ring-plot Analyses

The ring-plot analyses indicated that there was more old-forest around nest sites than around old-forest random points from 0.12 km through 1.36 km with significantly ($P < 0.05$) more old-forest from 0.09 km through 0.29 km, and suggestively ($P < 0.10$) more old-forest from 0.29 km to 0.65 km (Fig. 6a, b, and c). Beyond 1.36 km the amount of old-forest in rings around nest sites and old-forest random points was very similar (Fig. 6a and b).

Circle + Ring Analyses

The circle+ring analyses indicated that models adding the 1st, through 6th, and several of the rings from the 60th through 71st rings significantly ($P < 0.05$) contributed to the additional odds that the center point was a nest site (Fig. 7a and b). The coefficients for the 1st-6th (outer radii = 0.09-0.21 km) rings were positive and significant ($P < 0.05$) meaning that more old-forest in these rings increased the odds that the center point was a nest site (Fig. 7a and b). Conversely, the coefficients of the rings between the 60th and 71st rings (outer radii = 1.59 and 1.86 km respectively), were negative, and indicated that less old-forest in many of these rings significantly ($P < 0.05$) contributed to the odds that the center point was a nest site (Fig. 7a and b). In general, coefficients for the first ten rings (first 0.31 km away from nest) were positive and rings 11-200 (>0.31 km) were negative (Fig. 7b).

Figure 7b illustrated the additional odds (that the center of a circle was an owl nest site) associated with a 10% increase in the percent of old-forest in ring x+4, after

Figure 6. Old-forest in 200 concentric 100-m-wide ring-plots around spotted owl nest sites and old-forest random points. (a) percentage of old-forest[11], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of old-forest in $\text{ring}_{(x+4)}$ ($= 100[e^{(10)\beta} - 1]$).

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[11] For illustration of graph (a), only the data from every other plot size is shown.

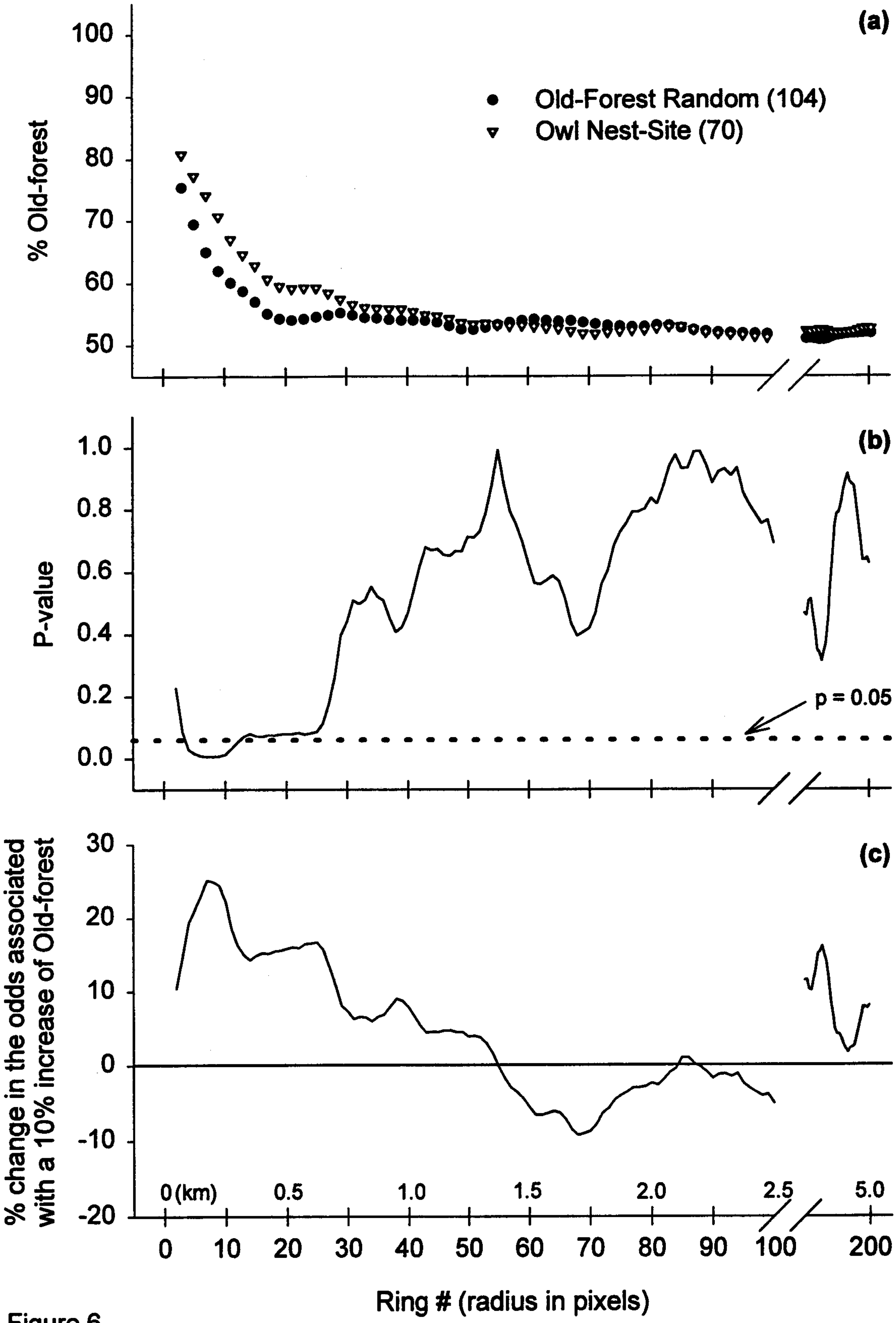
(a)
100
90
80
70
60
50
% Old-forest
● Old-Forest Random (104)
▽ Owl Nest-Site (70)
(b)
1.0
0.8
0.6
0.4
0.2
0.0
P-value
p = 0.05
(c)
30
20
10
0
-10
-20
% change in the odds associated with a 10% increase of Old-forest
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure 6.

Figure 7. Old-forest in 200 circle+ring plots around spotted owl nest sites and old-forest random points. (a) p-values associated with the $\text{ring}_{(x+4)}$ coefficient, (b) % change in the odds associated with a 10% increase of old-forest in $\text{ring}_{(x+4)}$ ($= 100[e^{(10)\beta} - 1]$).

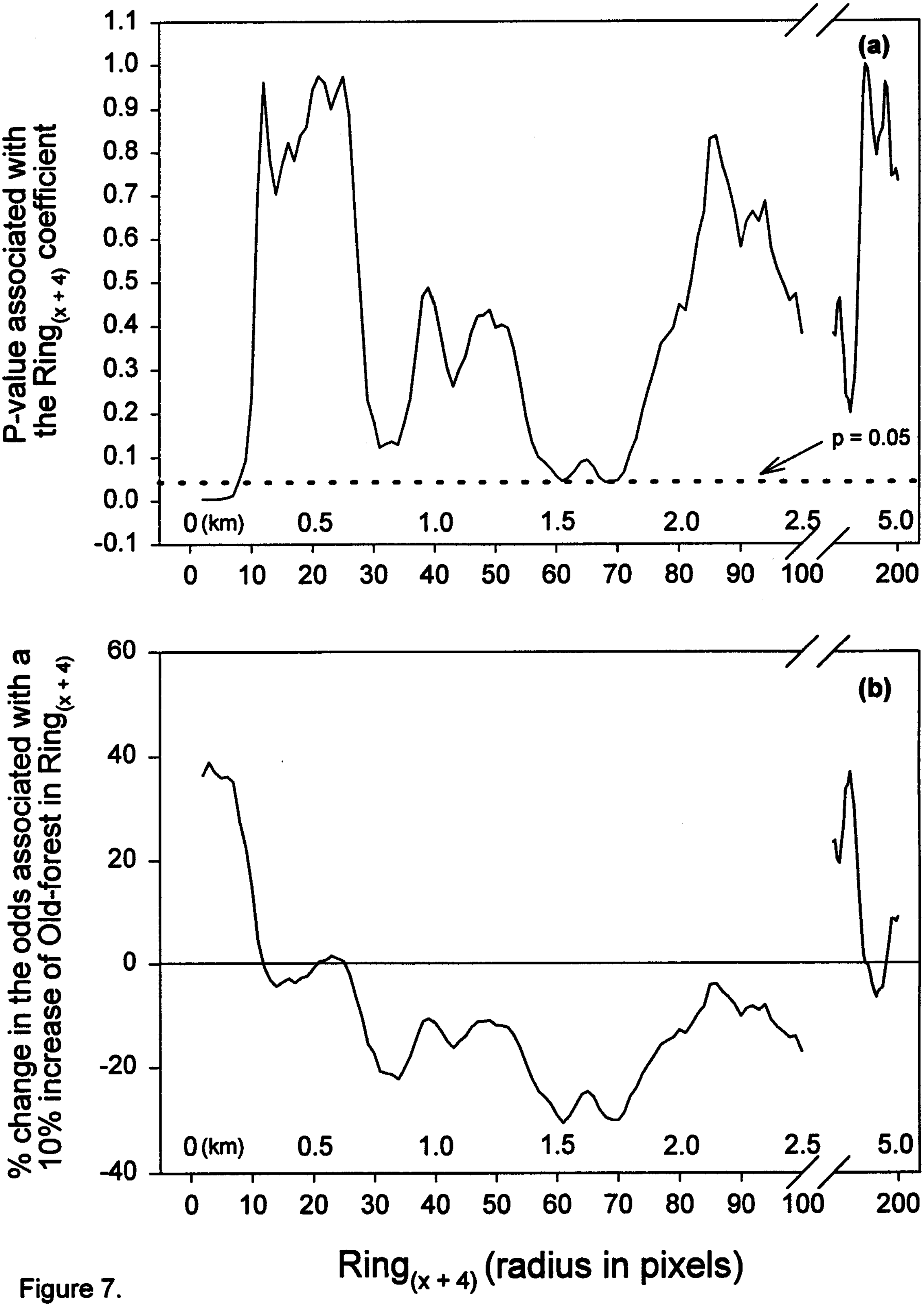
(a)
P-value associated with the Ring$_{(x+4)}$ coefficient
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
(b)
% change in the odds associated with a 10% increase of Old-forest in Ring$_{(x+4)}$
60
40
20
0
-20
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring$_{(x+4)}$ (radius in pixels)

Figure 7.

accounting for the amount of old-forest in circle x. For example: examine the case when Ring three (R3) was added on to Circle 2 (C2; Fig. 7b). An increase of 10% old-forest in R3 (given the amount in C2) yielded a 39% increase in the odds that the center point was a nest site. The corresponding plot of p-values associated with the ring-variable coefficients (Fig. 7a) illustrated that the R3 coefficient was highly significant ($P = 0.002$). Remember, when the odds were negative an increase in old-forest in the corresponding rings decreased the odds that the center point was a nest site. For example, look at the case C60+R61 in figures 7a and b. Holding the amount of old-forest constant in C60 we see that a 10% increase in R61 yielded a 31% decrease in the odds (Fig. 7b) that the center point was a nest site ($P = 0.045$; Fig. 7a).

DISCUSSION

Case-control studies using retrospective sampling and logistic regression are relatively new to the study of habitat association. However, their theory and application have been well developed in studying risk factors for diseases in the field of epidemiology (Ramsey et al. 1994). The use of such a design makes sense in human epidemiology because subjects (those contracting a specific disease) occur so rarely in the population at large, and because manipulative controlled studies are impossible (e.g., it would be impossible to select a group of people a priori and then wait to see who contracted a specific disease of interest) or unethical (e.g., it would be morally reprehensible to purposefully expose a selected group of people to a virus in order to test the factors that influence susceptibility). The extension of this approach to study northern spotted owl habitat association was straightforward both in structure and context of the problem. The structure was similar in that among all possible points on a landscape only a tiny proportion happened to be spotted owl activity centers or nest sites (rare occurrence, which calls for retrospective sampling). The context was analogous because northern spotted owls 1) are wild animals that use vast areas of forest (making timely controlled experiments that are uniform and repeatable impossible); and 2) are a "...threatened species...likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." (USDI 1988), making it ethically questionable to study in a manipulative fashion.

Owl Nest Sites vs. Totally Random Points

My results concur with those of previous studies conducted within the range of the northern spotted owl in the respect that there was more mature and old-growth forest around spotted owl nest-sites than was randomly available on the landscape

(Ripple et al. 1991a, 1997; Hunter et al. 1995; Lehmkuhl and Raphael 1993; Meyer et al., in review; Perkins et al., in review–Fig. 8). This pattern (more old-forest around owl points than around random points) holds throughout the owl's range, and occurs regardless of the general amount of old-forest available in each study area (as represented by the respective random point averages–the black circles on each graph) which ranged as low as 20.2% (largest plot of Perkins et al., in review) to as high as 51.7% (largest plots of this study and Ripple et al. 1991a; Fig. 8). In spite of the observational nature of these studies, collectively, they provide strong evidence that northern spotted owls consistently select portions of landscapes that are comprised of the highest amounts of old-forest available.

My finding that there was significantly more old-forest in circular plots up to 1.79 km radius was very similar to the findings of Hunter et al. (1995) who reported differences in plots up to 1.61 km in radius in northwestern California. However, other researchers found significantly more old-forest in larger plot sizes: 4.8 km in Olympic National Forest, Washington (Lehmkuhl and Raphael 1993), 3.4 km in the Central Cascades of Oregon (Ripple et al. 1991a), 2.4 km in southwestern Oregon (Ripple et al. 1997), and 2.4 km in the Central Coast Ranges of Oregon (Perkins et al., in review).

The results of my study closely matched those of Hunter et al. (1995) who also used a Landsat image to classify habitat, while all of the studies that found differences in amount of old-forest in larger plot sizes used aerial photos to classify habitat. The exceptionally large plots on the Olympic Peninsula may also be due to larger spotted owl home-ranges in that physiographic province (Thomas et al. 1990, Lehmkuhl and Raphael 1993). My results differed somewhat from those of Ripple et al. (1991a)

Figure 8. Comparison of amount of old-forest around northern spotted owl sites and random[12] points observed in the central Cascade mountains of Oregon with other similar studies throughout the owl's range. Physiographic provinces represented are: central Cascades of Oregon (a) and (c), Oregon Cascade foothills (b), Klamath Mountains (d) and (e), Oregon Coast Ranges (f) and (g), Olympic [National Forest], Washington (h), and northern California (I). Data are from: this study, comparing % "old-forest" class in 10 circular plots around 119 random points and 70 owl nest sites (a); Meyer et al. (in review) comparing % ["old-growth" + "mature"] classes around 10 random points and 10 owl nests (b), 21 random points and 21 owl nests (d), and 19 random points and 19 owl nests (f); Ripple et al. 1991a, comparing % "mature and old-growth" forest around 30 random points and 30 owl nests (c); Ripple et al. 1997, comparing % ["Open-canopy Old-conifer" + "Old-conifer"] classes around 20 random points and 20 owl nests (e); Perkins et al. (in review), comparing % ["Mature/young" + "Mature" + "Old/young" + "Old"] classes around 41 random points and 41 owl nests (g); Lehmkuhl and Raphael 1993, comparing % "total habitat" around 100 random points and 59 owl pair locations (h); and Hunter et al. 1995, comparing % "Mature and old-growth" around 50 random points and 33 nest sites (I). Asterisks indicate significant ($P < 0.05$) differences {for (a), (b), and (d)-(g) logistic regression where the response variable = 1 for nests or nest sites and 0 for random points and the single explanatory variable = the % [habitat]; for (c), (h) and (i) the significance levels represent results of the tests performed by the original authors}.

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[12] Several authors further restricted their random points: Hunter et al. 1995 excluded random points above 1,350 m elevation, Perkins et al. (in review) excluded random points falling in non-forest or within 1,260 m from known nests, Meyer et al. (in review) selected random points without replacement to avoid overlap of 3.4-km-radius plots.

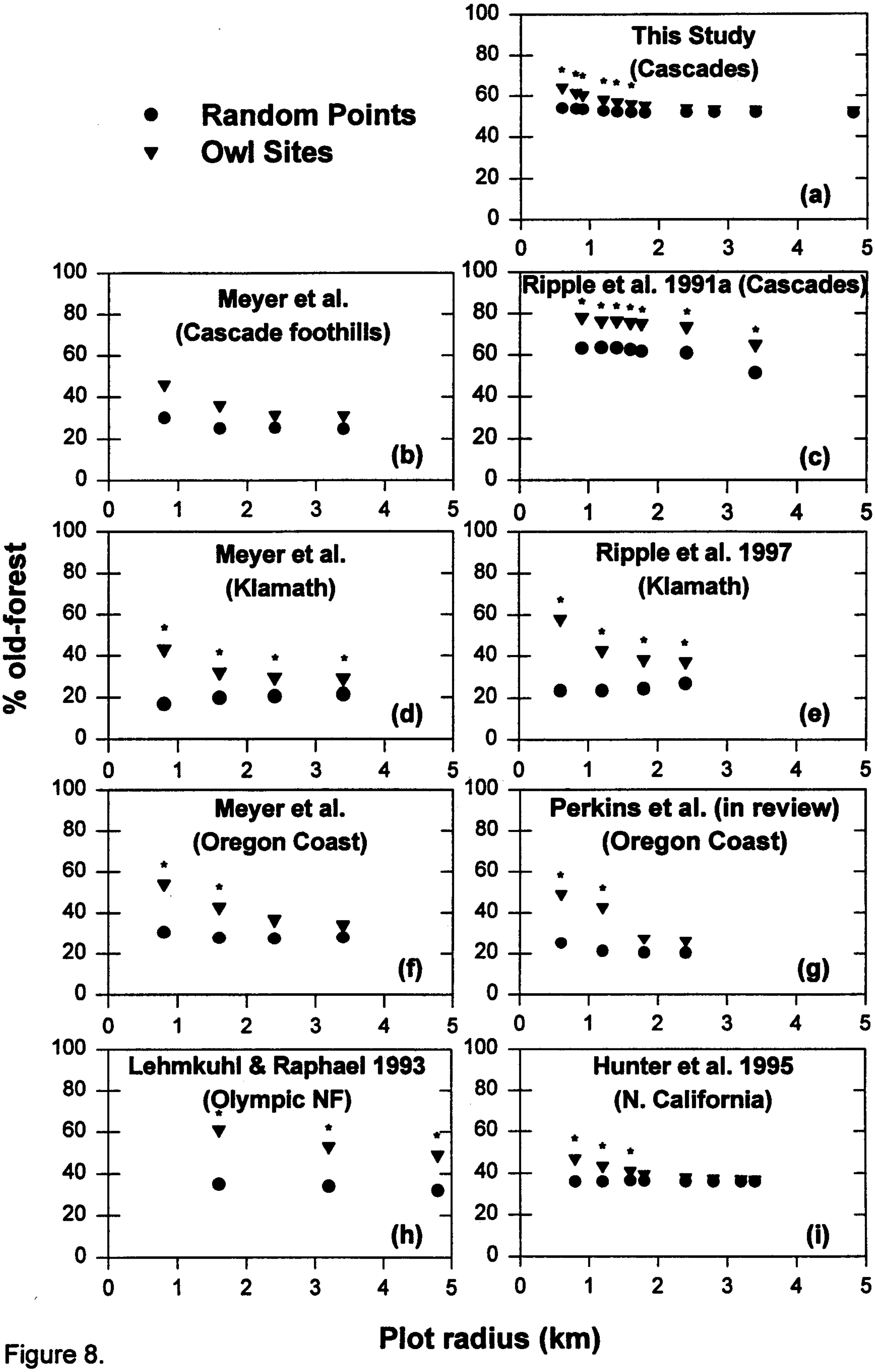
● Random Points
▼ Owl Sites
This Study (Cascades)
(a)
Meyer et al. (Cascade foothills)
(b)
Ripple et al. 1991a (Cascades)
(c)
Meyer et al. (Klamath)
(d)
Ripple et al. 1997 (Klamath)
(e)
Meyer et al. (Oregon Coast)
(f)
Perkins et al. (in review) (Oregon Coast)
(g)
Lehmkuhl & Raphael 1993 (Olympic NF)
(h)
Hunter et al. 1995 (N. California)
(i)
% old-forest
0
20
40
60
80
100
Plot radius (km)
0
1
2
3
4
5

Figure 8.

despite the fact that their study was in the same general area and used some of the same owl location data. They analyzed the amount of old-forest surrounding 30 owl nests and 30 random points in seven concentric circular plots from 0.6 km to 3.4 km in radius, and found significantly more old-forest in all seven plot sizes, compared to out to 1.79 km in this study. While a 1.79 km radius circle is a substantial area (975 ha) it is <30% as large as a 3.4-km radius (3,602 ha) circle. Additionally, Ripple et al. (1991a) estimated higher amounts of mature and old-growth forest around both nest sites and around random points.

My results differed from Ripple et al. (1991a) for several reasons. 1) My sample sizes were larger. 2) The study areas were defined differently (Fig. 9): their study area extended farther to the west and south and, my method of using the owl locations to define the study area boundaries reduced the potential for random points to fall on areas of the landscape that were not studied. Ripple et al. (1991a) allowed random points to fall anywhere on orthophoto quadrats that included an owl nest. This included substantial area to the west of the majority of their owl points. The combination of smaller sample sizes and their study area delineation technique resulted in a distribution of their random points slightly different than that of their owl locations. 3) My method for estimating the amounts of mature and old-growth forest differed from theirs. I used satellite coverage and a general classification system developed by other researchers [Cohen et al. 1995]. Cohen et al. (1995) did not have spotted owl biology and management specifically in mind when they classified their image, whereas Ripple et al. (1991a) did. As a result, Cohen et al.'s (1995) classification system did not specify different types or qualities of owl habitat. My regroupings of their original classes only partially achieved that goal. So, while the classification system that I used (based on spectral reflectance) was more objective than the techniques used by Ripple et al. (1991a–visual interpretation of aerial photos), it

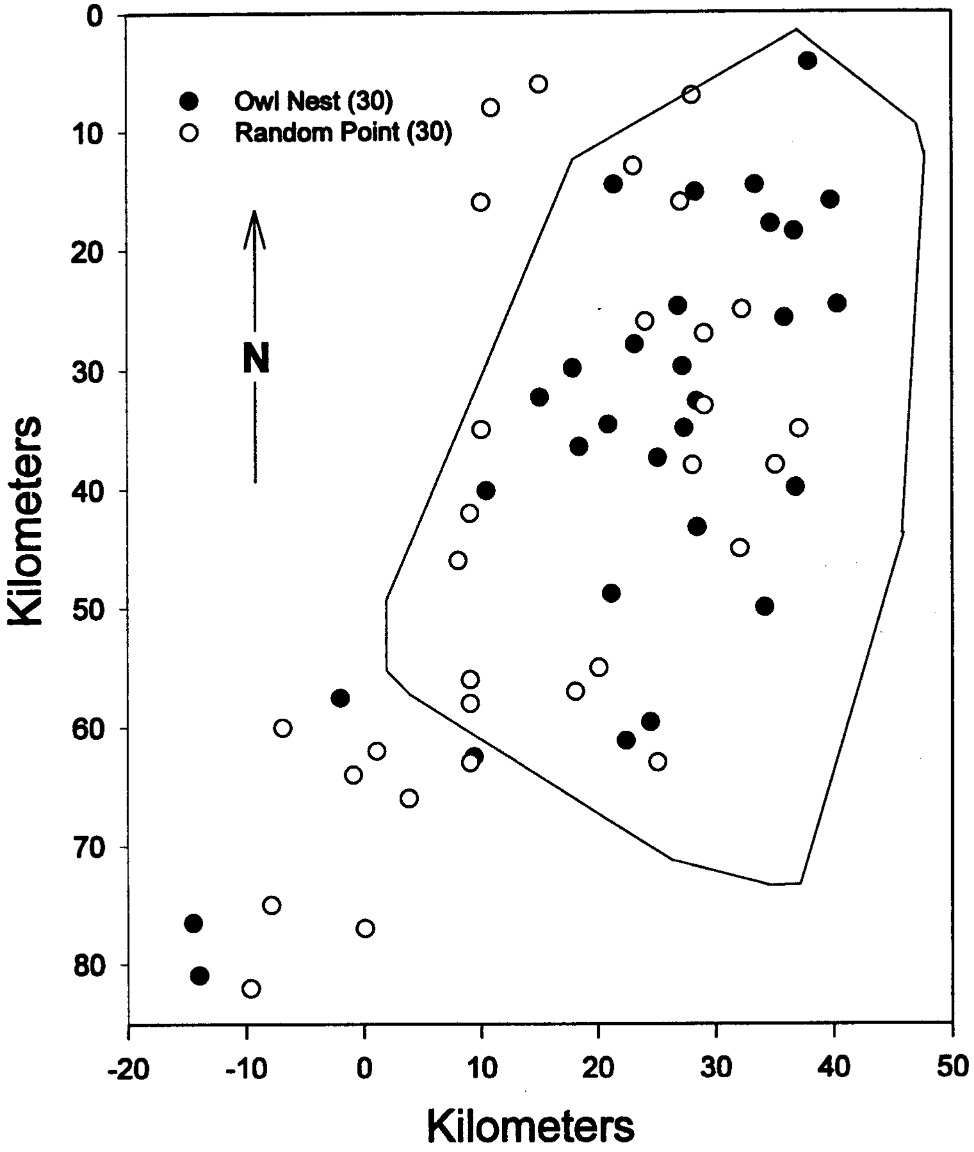

Figure 9. Points analyzed by Ripple et al. (1991a) relative to my study area.

was probably less accurate, especially for it's intended purpose. In spite of these inconsistencies, this study corroborated the general findings of Ripple et al. (1991a) in that there was a clear and strong association between northern spotted owl nest-sites and amount of old-forest in the Central Cascade Mountains of Oregon. Other researchers found similar results throughout the species' range (Lehmkuhl and Raphael 1993, Hunter et al. 1995, Ripple et al. 1997, Perkins et al., in review, Meyer et al., in review).

Owl Nest Sites vs. Old-forest Random Points

I remind the reader that the analyses addressed by the following discussion apply to habitat factors affecting the positioning or selection of owl nest sites on the landscape and do not address how these features affect owl fitness. For this reason, these data should not be used for making inferences regarding the amount or arrangement of habitat necessary for maintaining owl fitness.

As hypothesized, the amount of old-forest around owl nest-sites was similar in small plots, greater in medium-size plots, and similar in large plots to the amounts around points randomly drawn from old-forest (see Fig. 5a). These findings strongly support the idea that the influence of old-forest to nest site selection is greatest near the nest site and diminishes as distance from the nest increases. By necessity this suggests that spotted owl nest sites were associated with clumped (i.e., less fragmented) arrangements of old-forest. This was most obvious in the circle+ring analysis (Fig. 7b), where the ability to differentiate between owl nest sites and old-forest random points was improved by adding the information in sequential rings at two general landscape scales (or groups of plot sizes). First, more old-forest in the region within 200 m from a given point significantly increased the odds (or chance) that the point was an owl nest site[13]. Second, more old-forest in the band or region between approximately 1,500 and 1,800 m tended to significantly decrease the odds that the

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[13] For small-scale nest-site characteristics/relationships see Hershey 1996.

point was an owl nest site. Thus, owl nest sites differed on average from old-forest random points by having more old-forest in close rings surrounding them and less old-forest in outer rings surrounding them. This suggests a generally clumped arrangement of old-forest on landscapes centered on owl nests in contrast to more uniformly distributed old-forests around random points. Figure 10 illustrates this graphically--where landscapes A and B are both 50% forested, but landscape B differs in forest arrangement with more forest in the central circle, less forest in the outer ring, and identical amounts in the band in between. The fact that both comparisons (nest-sites vs. total random points and nest-sites vs. old-forest random points) tend to corroborate these findings (especially at the larger scales/plot sizes; Figs. A-3b and 7b) indicates that the landscapes surrounding owl nest sites are unique or anomalous compared to the general landscape. The circle+ring analyses have the statistically strongest results at the larger plot sizes where less old-forest in rings deciphers nest sites from both sets of random points. Perhaps on a landscape that was generally contiguous forest (i.e., patches are islands of younger forest in a matrix of older forest) the most discriminating feature was where forest was *not* present as opposed to where it *was* present.

A possible explanation for less old-forest beyond 1.5 km would be that owls selected nest sites at that scale, but it is difficult to believe that owls could have that large a frame of reference of their surroundings (making cognitive selection unlikely). It is, however, more plausible to think that those owls that succeeded at nesting (those in this study) did so, because they had sufficient resources (i.e., a threshold amount of old-forest-like habitat) energetically available to them. If owls select nest sites so as to maximize old-forest near the nest (or more likely, if a clumped arrangement of old-forest enables them to extract resources efficiently--thereby allowing nest initiation), then they also select nest sites with less old-forest at some distance from the nest by

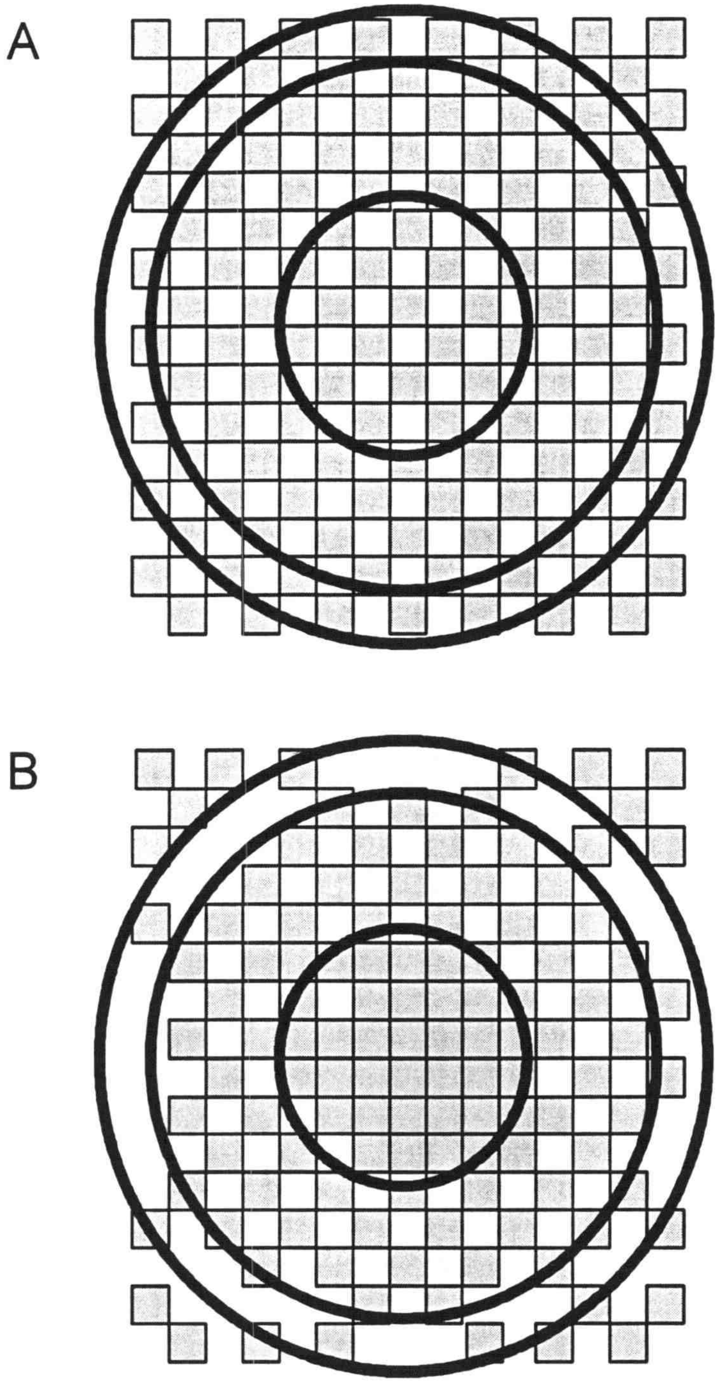

Figure 10. Hypothetical landscapes with 50% forest cover. Landscape (a) represents a uniform distribution of habitat, whereas, landscape (b) illustrates a landscape with more [relative to (a)] old-forest in the central circle, less in the outer ring and an identical amount in the band in between.

default. This is simply because there is a given amount of old-forest on the landscape, that is not uniformly distributed. Therefore, if there are higher than average amounts of old-forest near a given point, then there must be lower than average amounts of old-forest beginning at some distance as you move away from that point.

Unfortunately, the design of this study (observational) did not enable me to exclude alternative explanations for more old-forest within 25-30 ha and less old-forest > 1.5 km from owl nests. For example, 1.5 km corresponds to 0.93 miles (close to 1 mile). Perhaps land managers of the Willamette National Forest have been disproportionately cutting areas at that distance from known owl nest locations. This is unlikely since, such landscape planning needed to occur between 1977 (when the Regional Forester agreed to protect spotted owl habitat in accordance with the interim recommendations of the Oregon Endangered Species Task Force–Thomas et al. 1990, Meslow 1993) and 1988 (the year of the image used for this study). While some of the pairs studied were undoubtedly affected by the recommendations, it is doubtful that many experienced planned harvests at the discrete distances I observed because no corresponding distances or minimum required acreages were called for in management plans of that period.

It is intuitive that one or both of the other two habitat classes (young forest, and non-habitat) would display an opposite pattern to old-forest–at scales where there is more old-forest around owl nest sites there must be less young forest and/or non-habitat. This appeared to be true for both classes and is discussed in the Appendix.

General Discussion

Though concentric circle-plot analyses can be very useful to land managers faced with making decisions for lands with spotted owl habitat, they have been criticized for lacking independence across scales (Ramsey et al. 1994) because a circle of given size includes all circles of smaller size. Because of this plot arrangement, a habitat difference detected at large plot sizes might be an artifact of a difference occurring at the smaller plot sizes (Ramsey et al. 1994). Therefore, non-overlapping ring-plots can provide additional information because they are more spatially independent (though not entirely). The ring-plot analyses supported this logic by indicating that observed differences in the amount of old-forest were most dramatic in rings of a smaller maximum size than was detected in circle-plots.

The circle+ring analyses represented a third step in refining the ability to decipher the spatial scales most important for spotted owl habitat association. This analysis allowed holding the amount of old-forest in the central (circle) portion of a given plot constant and ask: "How does the addition of new information (amount of old-forest in one ring) add to the model's predictive capability?", and provided insight that was not readily apparent in the individual concentric circle, and concentric ring analyses alone. However, I believe that the third analysis was most useful and interpretable biologically when given the context provided by the circle-only and ring-only analyses.

The trend of increased association (importance?) of old-forest with decreased distance from the nest is biologically intuitive, from an energetics standpoint, for central-place foraging species like spotted owls (Carey and Peeler 1995). Additionally, the requirement of large areas of old-forest habitat is also understandable for a species that tends to specialize on medium-sized prey items that occur at low densities

(Forsman et al. 1984; Rosenberg and Anthony 1992; Carey et al. 1991, 1992; Carey 1993) especially on a dichotomous landscape that largely consists of unmanaged older forests and young plantations (generally unused by spotted owls). How or if the association with amount and arrangement of old-forest extends to reproductive performance (and other measures of owl fitness; Noon and Biles 1990, Murphy and Noon 1992) remains unclear. Though reproductive data were not included in these analyses, comparison of the amount of old-forest around the 70 activity centers that had nest sites versus 14 sites that did not during the study showed that the percentage of old-forest around nests averaged slightly higher ($P \leq 0.10$ in many plots; Figs. 11a and b). The odds that a pair nested during the study increased by as much as 50% with a 10% increase in the amount of old-forest. Though preliminary, this exploratory analysis indicates that there may be a relationship between the amount of old-forest and owl productivity.

Circular plots inadequately describe actual spotted owl home-ranges. However, when compared to radio-telemetry (which can be prohibitively expensive and ethically questionable for a federally Threatened species--see Foster et al. 1992), circular plots are economical and easy for land managers to use. For these reasons researchers have demonstrated the feasibility of using circular plots in place of radio-telemetry studies (see Lehmkuhl and Raphael 1993). Circular plots should be most adequate in physiographic provinces that have the most habitat and are least fragmented (like the Oregon Cascades--Thomas et al. 1990, USDI 1992, Miller et al. 1996) because owl nest sites seem to be centrally located within home-ranges in such areas (Forsman 1980). Nevertheless, circles are not realistic surrogates of actual home-ranges. One way to account for the added variability caused by using circles is to employ large samples (as in this study).

Figure 11. Old-forest in 200 concentric circle-plots around 14 non-nesting owl activity centers compared to 70 activity centers with nest sites, central Cascade mountains, Oregon (1987-1995). (a) percentage of old-forest[14], (b) p-values for logistic regressions of nest sites vs. non-nest sites, (c) % change in the odds of nesting associated with a 10% increase of old-forest ($= 100[e^{(10)\beta} - 1]$).

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[14] For illustration of graph (a), only the data from every other plot size is shown.

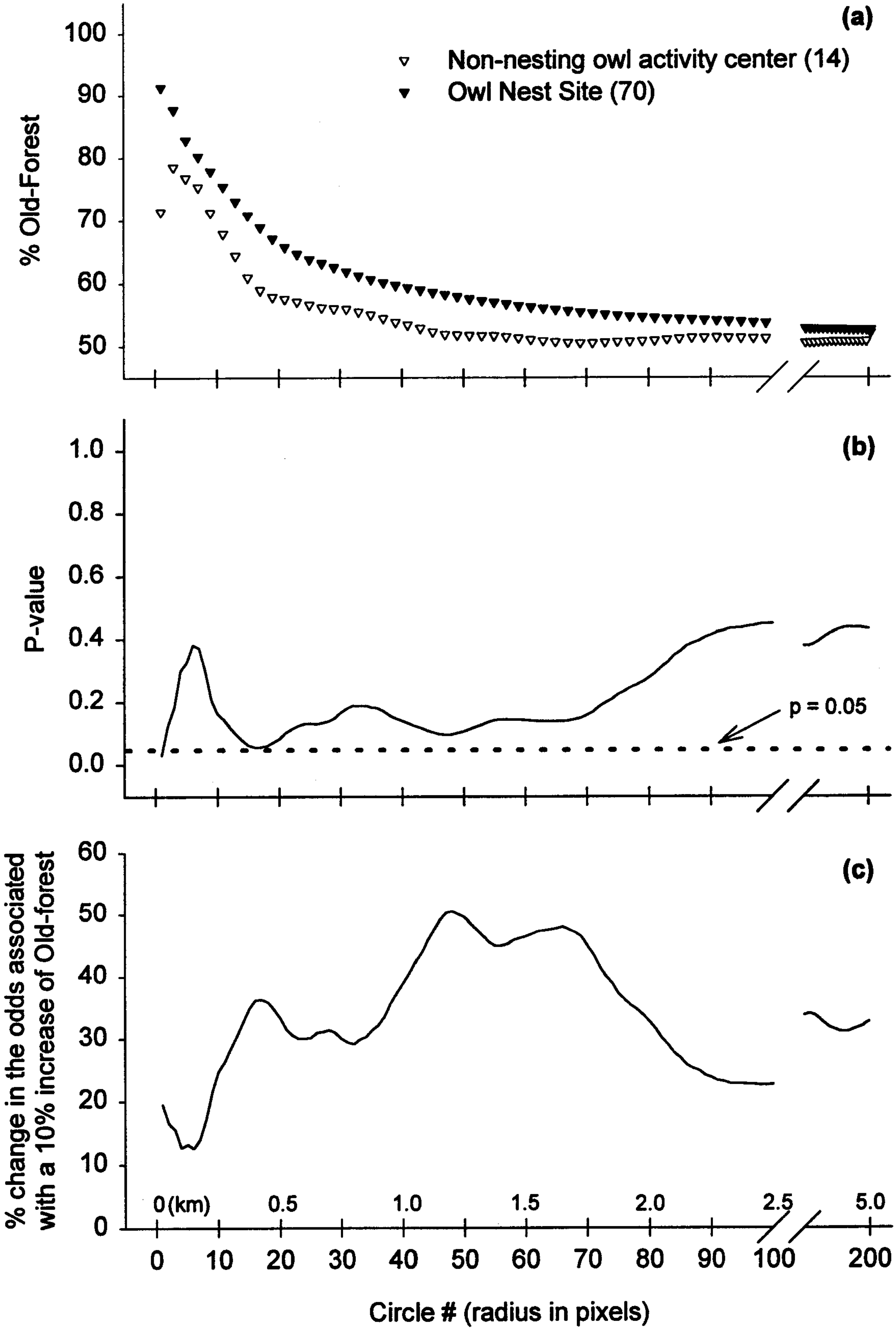
(a)
100
90
80
70
60
50
% Old-Forest
▽ Non-nesting owl activity center (14)
▼ Owl Nest Site (70)
(b)
1.0
0.8
0.6
0.4
0.2
0.0
P-value
p = 0.05
(c)
60
50
40
30
20
10
0
% change in the odds associated with a 10% increase of Old-forest
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure 11.

CONCLUSIONS

This was an observational study of habitat association. Consequently, all inferences are associative, *not* causative. However, the analytic tools employed were powerful for detecting patterns in the data. Such an approach was necessary for studying a species that was rare and/or otherwise difficult to use in controlled, manipulative experiments.

This study included the largest sample sizes used for any within-physiographic province habitat association study to date and yielded several important results. First, the comparison of owl nest-sites and totally random points reaffirms the strong association between northern spotted owls and mature and old-growth forests (detected previously by Forsman 1980; Forsman et al. 1984; Carey et al. 1990; Ripple et al. 1991a, 1997; Bart and Forsman 1992; Lehmkuhl and Raphael 1993; Hunter et al. 1995; Perkins et al., in review). Second, the comparison of owl nest sites and points randomly drawn from old-forest indicated that in addition to the amount, the arrangement of old-forest habitat was important (and served as a good predictor) for spotted owl occupancy and nest site selection/positioning. Third, the spatial scale at which nest-site positioning was most associated with the amount of old-forest was within the first 15-30 ha (200-300-m radius) surrounding the nest site. Fourth, the relative lack of old-forest habitat around owl nest sites > 1.5 km also served as a good predictor of owl nest-site locations. This may indicate selection of very large areas with the highest amounts of old-forest available on a landscape, however, the observational design of this study did not exclude alternative conclusions (e.g., land managers may have been purposefully harvesting away from known nest sites). Lastly, the degree to which the owl is considered an interior species depends both upon the definition and the spatial scale employed. Obviously, owls have been shown to forage and even nest up to or on the edge of clear-cuts or other non-forested patches. In this sense, northern spotted owls may not be interior species, however, the fact that they are associated with high proportions of old-forest habitat that tends to be centrally arranged around nest-sites does indicate a tendency toward some level of interior behavior. Rather than avoiding edge, owls may simply prefer or require large amounts of old-forest in close proximity for efficient foraging.

These findings strictly apply to spotted owl nest site selection/positioning and do not imply the amount of habitat necessary for site-specific spotted owl persistence and/or reproduction. Additionally, these findings apply to the owl population in the central Willamette National Forest, and perhaps may be extended to the larger Oregon Cascades Physiographic Province (as described in USDI 1992). These findings, both in terms of habitat association and habitat arrangement, depended on the dichotomous nature of the habitat conditions in the study area: forests tending to be either very young (non-habitat) or very old (structurally and biologically complex) and relatively uniform within patches. These associations will likely prove more difficult to demonstrate in regions where 1) there are more intermediate-aged forests, and 2) where uneven aged forests are common (because of human induced or natural disturbance regimes).

The results may be conservative in terms of spatial scale for several reasons: 1) while typical of federal lands (excluding Wilderness) in the Oregon Cascades, the studied landscape had few or no unfragmented areas, thus in a fairly uniformly fragmented landscape owls were associated with more old-forest than was generally available. 2) The recommendations were based on an alpha level of 0.05 which is conservative in itself and is sensitive to sample size (i.e., significance would likely increase in larger plot sizes/spatial scales with greater sample sizes). 3) My habitat classification was based on satellite imagery which was arguably less accurate than aerial photo interpretation and appeared to yield lower (conservative) estimates of old-forest habitat. Lastly, because owls exhibit high affinity and tenacity toward home-ranges and favored nest locations, they may continue to reside and nest in specific locations in spite of adjacent habitat alterations subsequent to original selection of the site. In other words, owl pairs may select a particular nest site prior to (perhaps as much as a decade before) habitat alteration and then continue to use that site even if conditions affecting their survival and reproductive potentials (or those of their young) have changed.

Management Recommendations

The common assumptions that 1) a core area is important for northern spotted owls, and 2) sensitivity to habitat loss increases as distance to the nest site decreases are supported by this study. Thus, it appears that both the amount *and* arrangement of habitat impinge upon the biology of northern spotted owls. This study suggests that the landscape scales of most importance to owl nest-site selection/positioning when considering the proportion of old-forest appear to be (in descending order): the first 10-15 ha (≈200-m radius) {results from model 3}, the first 25-30 ha (≈300-m radius) {results from model 2}, the first 200 ha (800-m radius){results from model 1} and possibly the first 700 ha (1,500-m radius) {results from model 3} surrounding a given nest site. Because, in the nine-year study individual owl pairs used as many as five different nest trees (within a 10-ha area), it appears important to provide core areas large enough for multiple nest sites. The exact spatial results reported above are specific to owls in this study area and are likely to be different for other physiographic provinces. However, it is intuitive that the general trend, of increased association with structurally complex habitat with decreased distance from the nest, might apply to other portions of the subspecies' range.

It is extremely important to realize that these results do not indicate that old-forest habitat beyond 800 m from a nest site is unimportant to spotted owls. In this study area, mean home-range size was nearly 1,800 ha (MCP, Miller and Meslow 1989) which is approximated by a circular area of 2,400 m (2.4 km) in radius. Thus, owls in this area, use old-forest habitat > 1,000 m from the nest site. The degree to which old-forest habitat beyond this distance is important or is offset by higher amounts of habitat ≤ 1,000 m is unknown.

Research Recommendations

My study indicates that the issue of scale must be addressed when attempting to assess the association between northern spotted owls and old-forest arrangement and may further illustrate the appropriate spatial scales to use for such inquiry. Future research should address how forest composition affects northern spotted owl reproduction and survival.

In general, this study corroborated the findings of all previous spotted owl habitat association studies. However, the specific discrepancies between this study and Ripple et al. (1991a) indicate that: large sample sizes (requiring long-term studies with large spatial extent), analysis tools allowing scale-specific inferences, and well defined methods of study-area delineation and habitat classification, are important elements for assessment of the effects of habitat fragmentation on northern spotted owls.

This study used larger sample sizes and a more specific delineation of study area boundaries than did Ripple et al. (1991a). While Ripple et al. (1991a) used an intuitive and valid approach for defining their study area, the combination of study area definition and a relatively small sample size contributed to somewhat different spatial conclusions. I recommend that study areas be defined by the owl locations themselves, as in this study. I am uncertain as to the effects of "over-sampling" an area spatially with numerous overlapping plots. More work should be conducted with spatial models to assess the potential effects of sampling real landscapes with different random sampling schemes (e.g., with replacement vs. without, with overlapping vs. non-overlapping plots). Lastly, attention should be given to the comparability of different methods of habitat classification.

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APPENDIX

The following figures illustrate the data presented in the main body of the text using non-overlapping, 25-m-wide rings. Additionally, figures A-7 through A-18 address the other terrestrial cover types (young and non-habitat) and represent additional analyses and information that were useful but not essential for the main focus of the thesis. However, they are helpful background for interpreting it's results and conclusions. It is intuitive that one or both of the other two habitat classes (young forest, and non-habitat) would display an opposite pattern to old-forest: at scales where there is more old-forest around owl nest sites there must be less young forest and/or non-habitat. This appeared to be true for both classes. I took the liberty to include text (in italics) describing the results of each figure in its respective legend.

Figure A-1. Old-forest in 200 concentric circle-plots around spotted owl nest sites and totally random points. (a) percentage of young forest[15], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$).

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[15] For illustration of graph (a), only the data from every other plot size is shown.

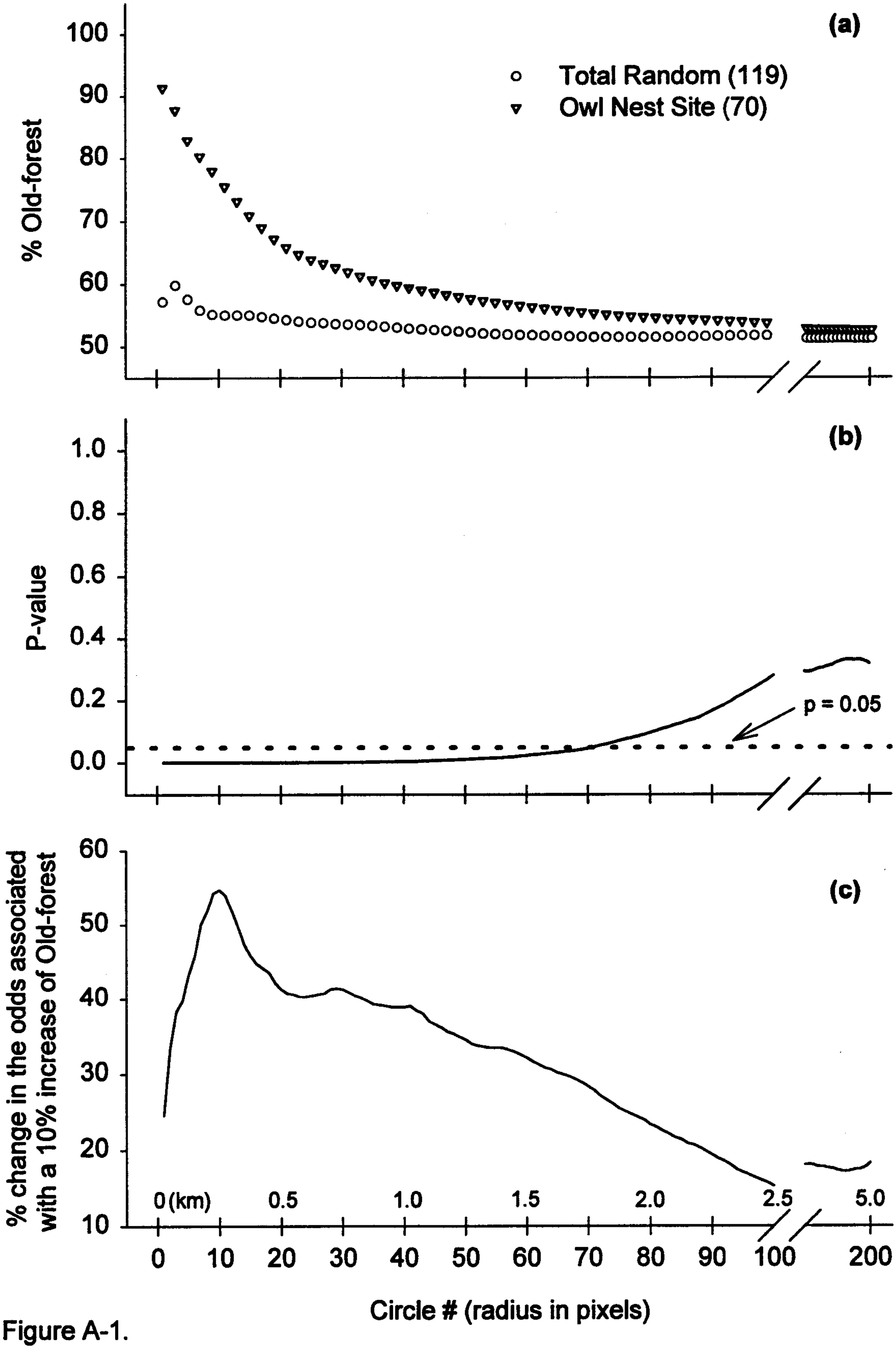
(a)
% Old-forest
100
90
80
70
60
50
○ Total Random (119)
▿ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of Old-forest
60
50
40
30
20
10
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure A-1.

Figure A-2. Old-forest in 200 concentric non-overlapping ring-plots around spotted owl nest sites and totally random points. (a) percentage of young forest[16], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$). *There was more old-forest around owl nest-sites in ring-plots up to 2.22 km in radius, with significantly more (*$P > 0.05$*) in all plots smaller than 0.72 km in radius. At plot sizes larger than 2.68 km in radius, the amount of old-forest in ring-plots around owl nest-sites was either equal or slightly (non-significantly;* $P > 0.05$*) more than around random points.*

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[16] For illustration of graph (a), only the data from every other plot size is shown.

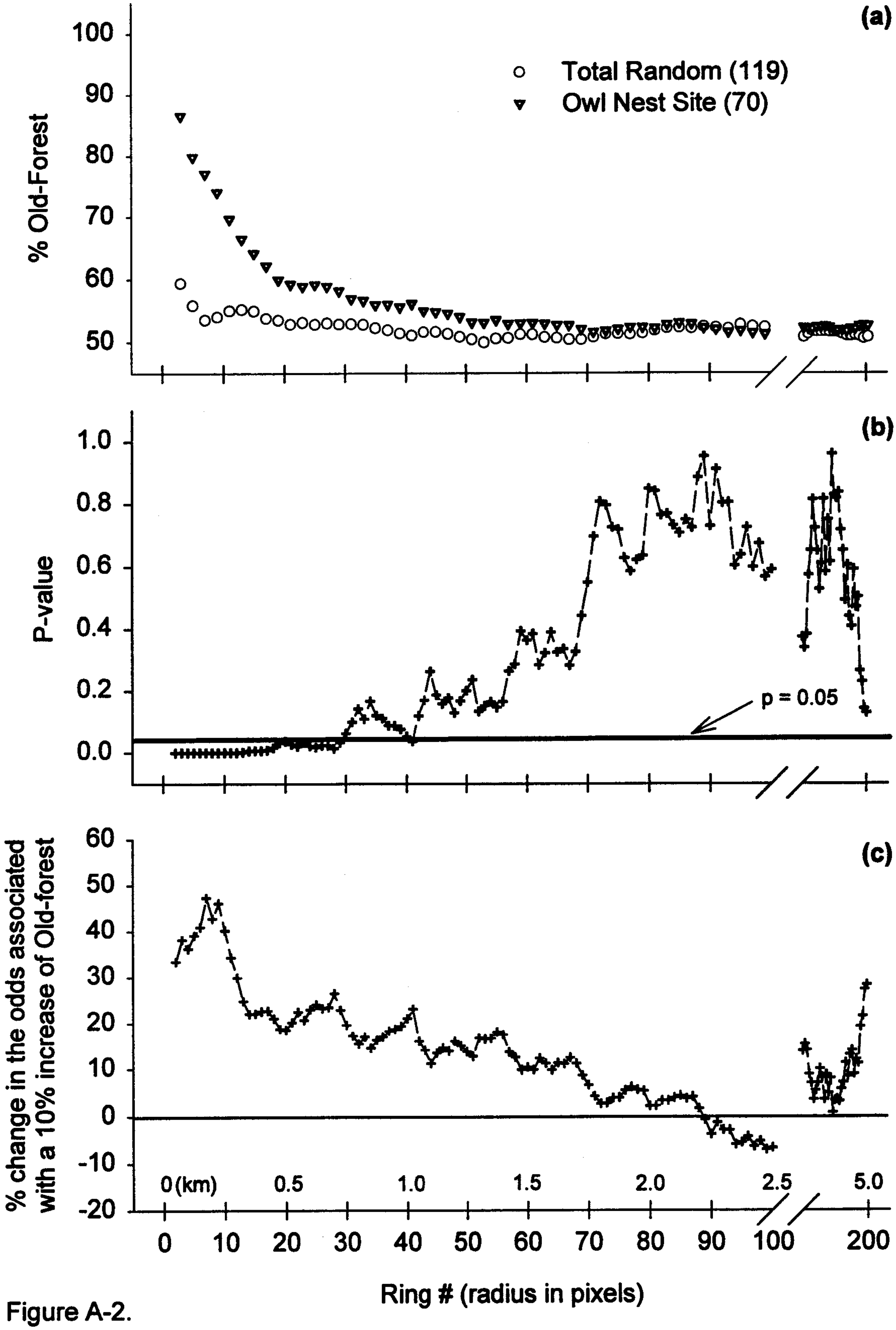
(a)
% Old-Forest
100
90
80
70
60
50
○ Total Random (119)
▼ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of Old-forest
60
50
40
30
20
10
0
-10
-20
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure A-2.

Figure A-3. Old-forest in 200 circle + ring plots around spotted owl nest sites and totally random points. (a) p-values associated with the ring$_{(x+1)}$ coefficient, (b) extra odds associated with a 10% increase in young forest in ring$_{(x+1)}$ (= $100[e^{(10)\beta} - 1]$).

The circle+ring analyses indicated that models adding the 1st through the 5th, 11th, 68th through 73rd, 77th through 81st, and 86th through 100th rings significantly ($P \leq 0.05$) *contributed to the additional odds that the center point was a nest site. The coefficients for the 1st-7th (outer radii = 0.12-0.24 km), 117th-123rd (outer radii = 3.01-3.16 km), 127th-170th (outer radii = 3.28-4.38 km), and 191st-192nd rings (4.91-5.00 km) tended to be positive meaning that more old-forest in these rings increased the odds that the center point was a nest site but none were significant* ($P > 0.05$)*. Conversely, the coefficients for all other ring variables tended to be negative, with most of those between the 68th-100th (1.79-2.60 km) significantly* ($P < 0.05$) *so, indicating that less old-forest in these rings contributed to the odds that the center point was a nest site.*

Figure A-3b represents the additional odds (that the center of a circular plot was an owl nest site) that were associated with a 10% increase in the amount of old-forest in ring x+4, after accounting for the amount of old-forest in circle x. In other words, after accounting for the amount of old-forest in the circle (central portion of each plot) of radius x, how did the additional information (% old-forest) in the single ring with radius x+4 contribute to distinguishing nest-sites from random points? For example: In (a) and (b) examine the case when ring four (R4; inner radius = 3 pixels, outer radius = 7 pixels or 0.19 km) was added to circle three (C3; radius = 3 pixels or 0.06 km). An increase of 10% old-forest in R7 yielded a 27% increase in the odds that the center point was a nest site (b). The corresponding plot of p-values associated with the ring-variable coefficients (a) illustrated that the R4 coefficient was significant ($P = 0.019$)*. Notice that when the extra odds were negative, more old-forest in the rings decreased the odds that the center point was a nest site. For example, look at the case C92+R93 (circle radius, inner-ring radius = 2.32 km, outer-ring radius = 2.42 km respectively) in (b). For a given amount of old-forest in C92, increasing the amount in R93 by 10% yielded a 43% decrease in the odds that the center point was a nest site (the coefficient for R93 was significant [*$p = 0.011$*]; (a).*

From these figures we see that more old-forest in rings 2-6 (outer radii = 0.12 km-0.21 km) yielded significant increases in the additional odds that the center point was a nest site (after accounting for the amount of old-forest in the inner portions [circles]). However, more old-forest in most of the rings R70-R101 (1.76-2.55 km) yielded significant ($P < 0.05$) *decreases in the additional odds that the center point was a nest site. These observations are put in perspective by revisiting the % old-forest profile plots for circles and rings (Figures A-1a and A-2a respectively). Figure A-2a shows that the amount of old-forest in ring-plots around owl nest-sites became similar to the amount around random points at about ring 70 (1.54 km). This corresponds to the plot size at which Figure A-3b indicated that increased amount of old-forest in these rings significantly decreased the additional odds that the center point was a nest site.*

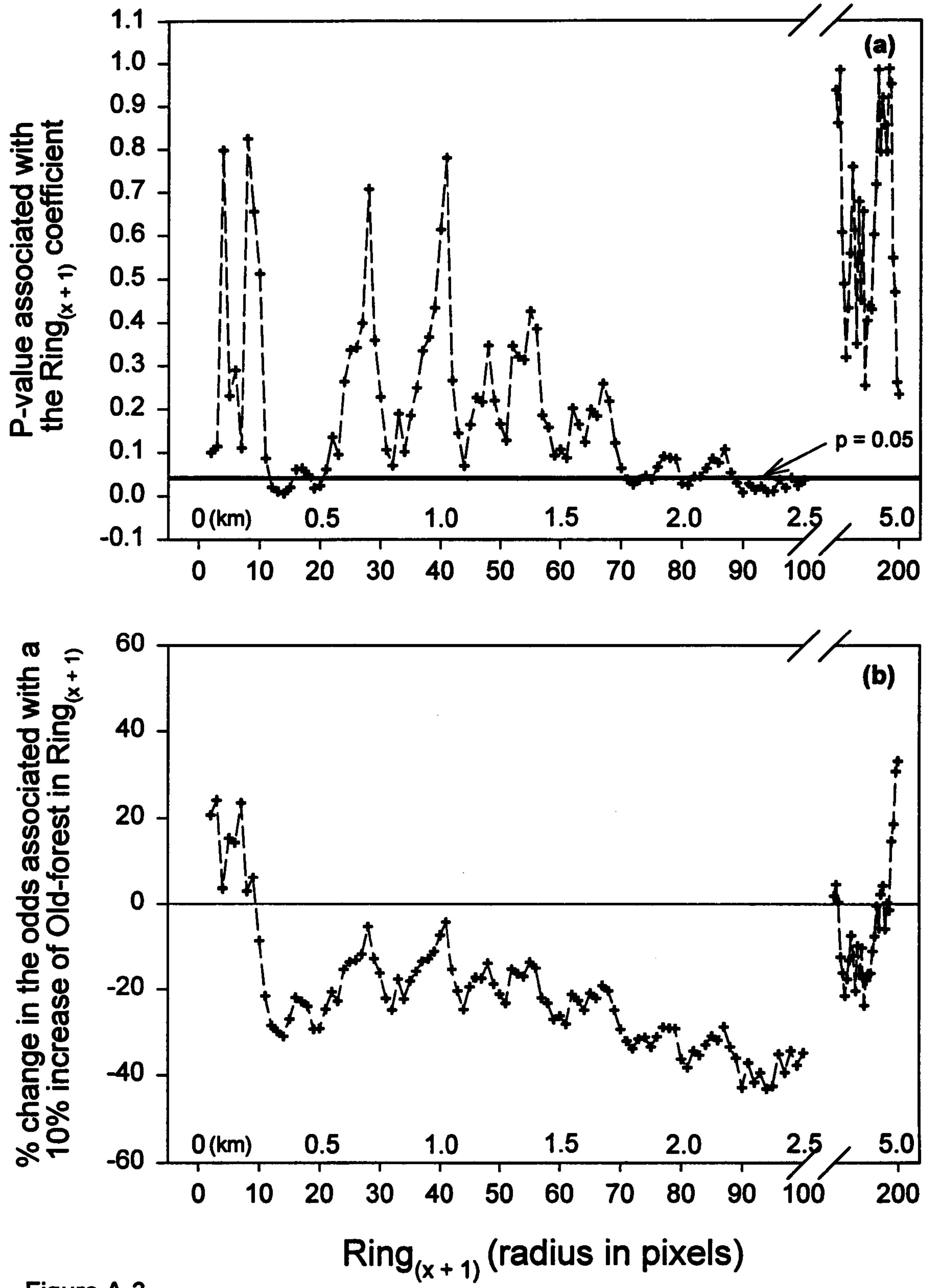
(a)
P-value associated with the $\text{Ring}_{(x+1)}$ coefficient
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
(b)
% change in the odds associated with a 10% increase of Old-forest in $\text{Ring}_{(x+1)}$
60
40
20
0
-20
-40
-60
$\text{Ring}_{(x+1)}$ (radius in pixels)

Figure A-3.

Figure A-4. Old-forest in 200 concentric circle-plots around spotted owl nest sites and old-forest random points. (a) percentage of young forest[17], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$).

---

[17] For illustration of graph (a), only the data from every other plot size is shown.

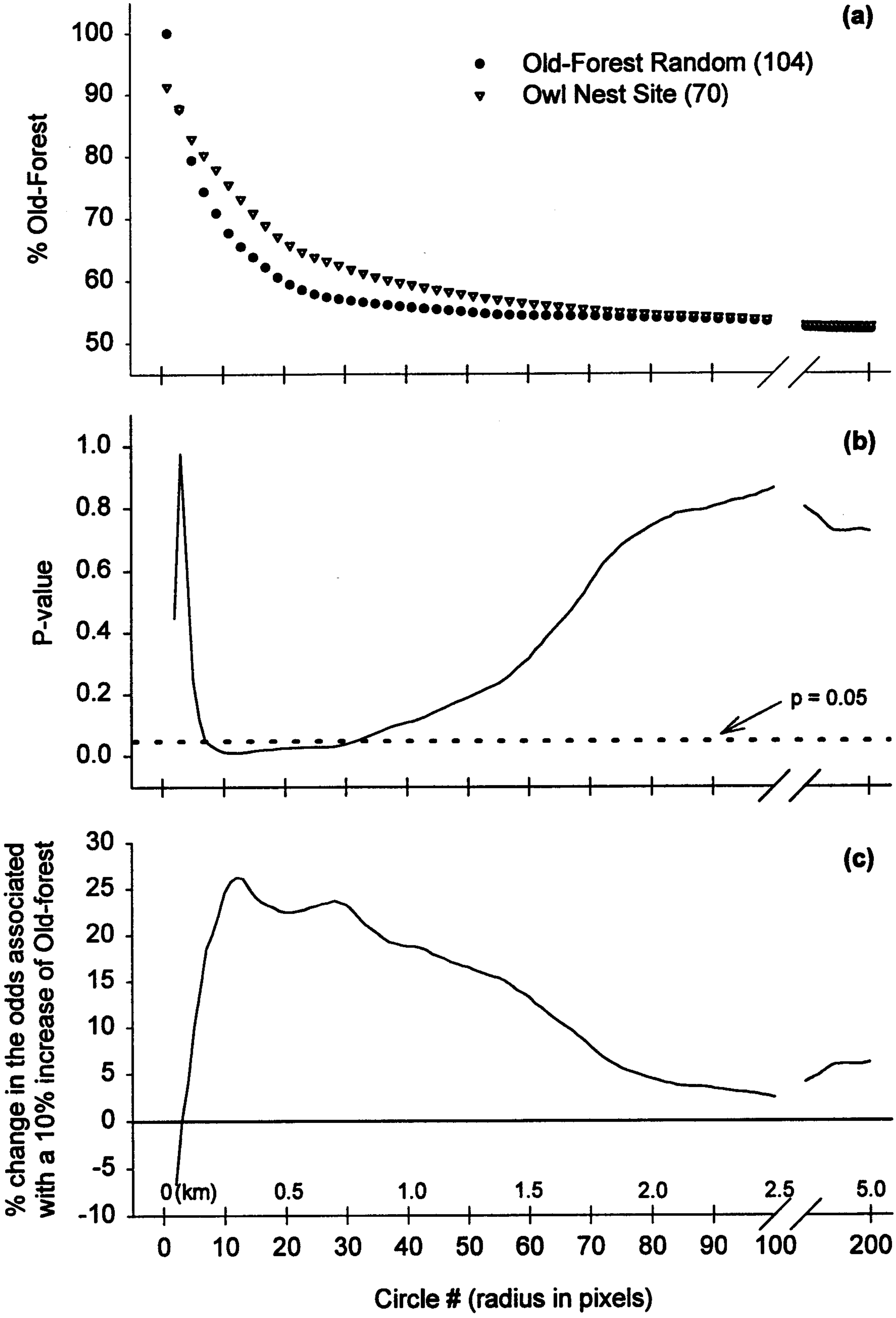
(a)
● Old-Forest Random (104)
▿ Owl Nest Site (70)
% Old-Forest
100
90
80
70
60
50
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of Old-forest
30
25
20
15
10
5
0
-5
-10
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure A-4.

Figure A-5. Old-forest in 200 concentric non-overlapping ring-plots around spotted owl nest sites and old-forest random points. (a) percentage of young forest[18], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$).

---

[18] For illustration of graph (a), only the data from every other plot size is shown.

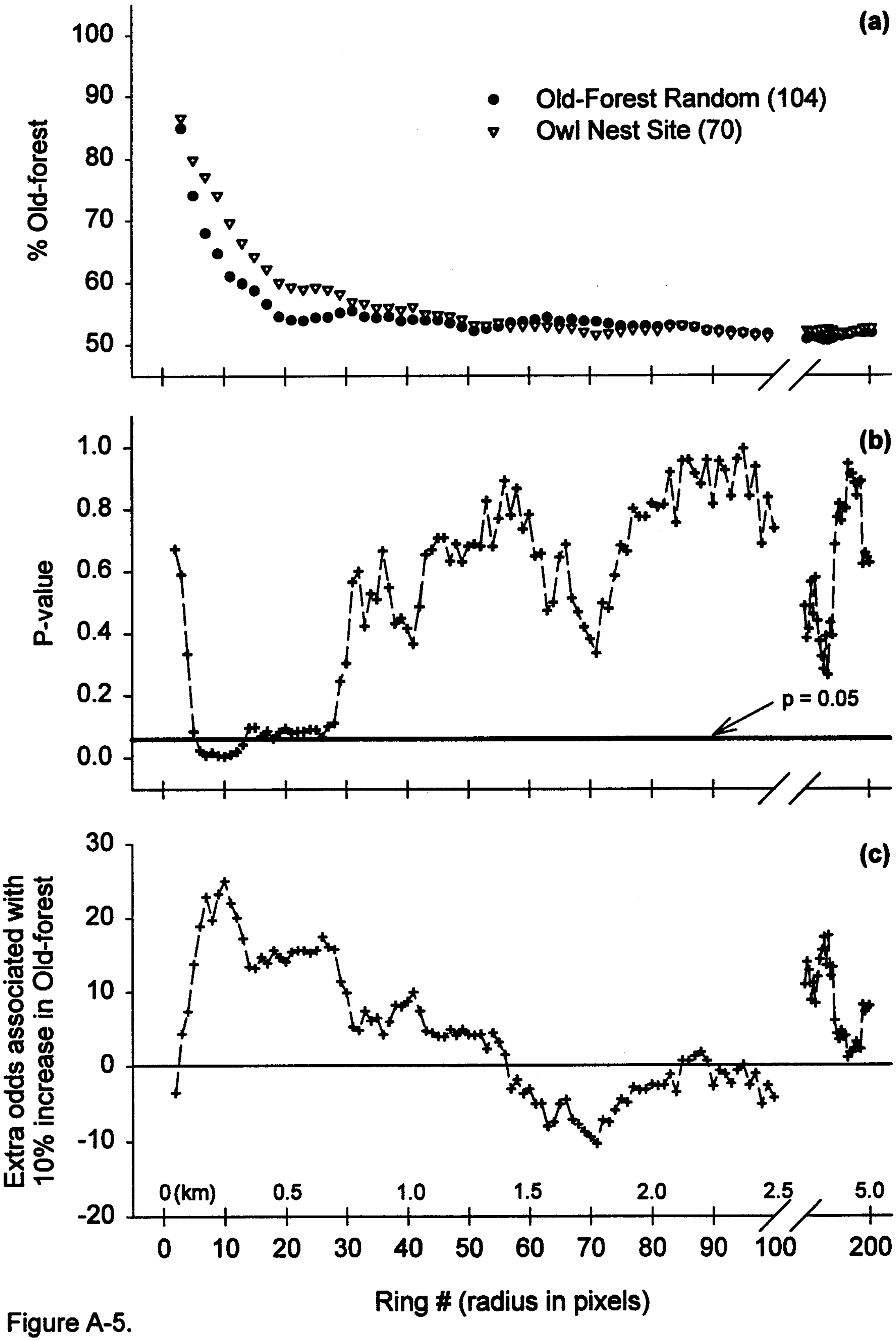
(a)
% Old-forest
100
90
80
70
60
50
● Old-Forest Random (104)
▿ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
Extra odds associated with 10% increase in Old-forest
30
20
10
0
-10
-20
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure A-5.

Figure A-6. Old-forest in 200 circle+ring plots around spotted owl nest sites and old-forest random points. (a) p-values associated with the $\text{ring}_{(x+1)}$ coefficient, (b) extra odds associated with a 10% increase in young forest in $\text{ring}_{(x+1)}$ ($= 100[e^{(10)\beta} - 1]$).

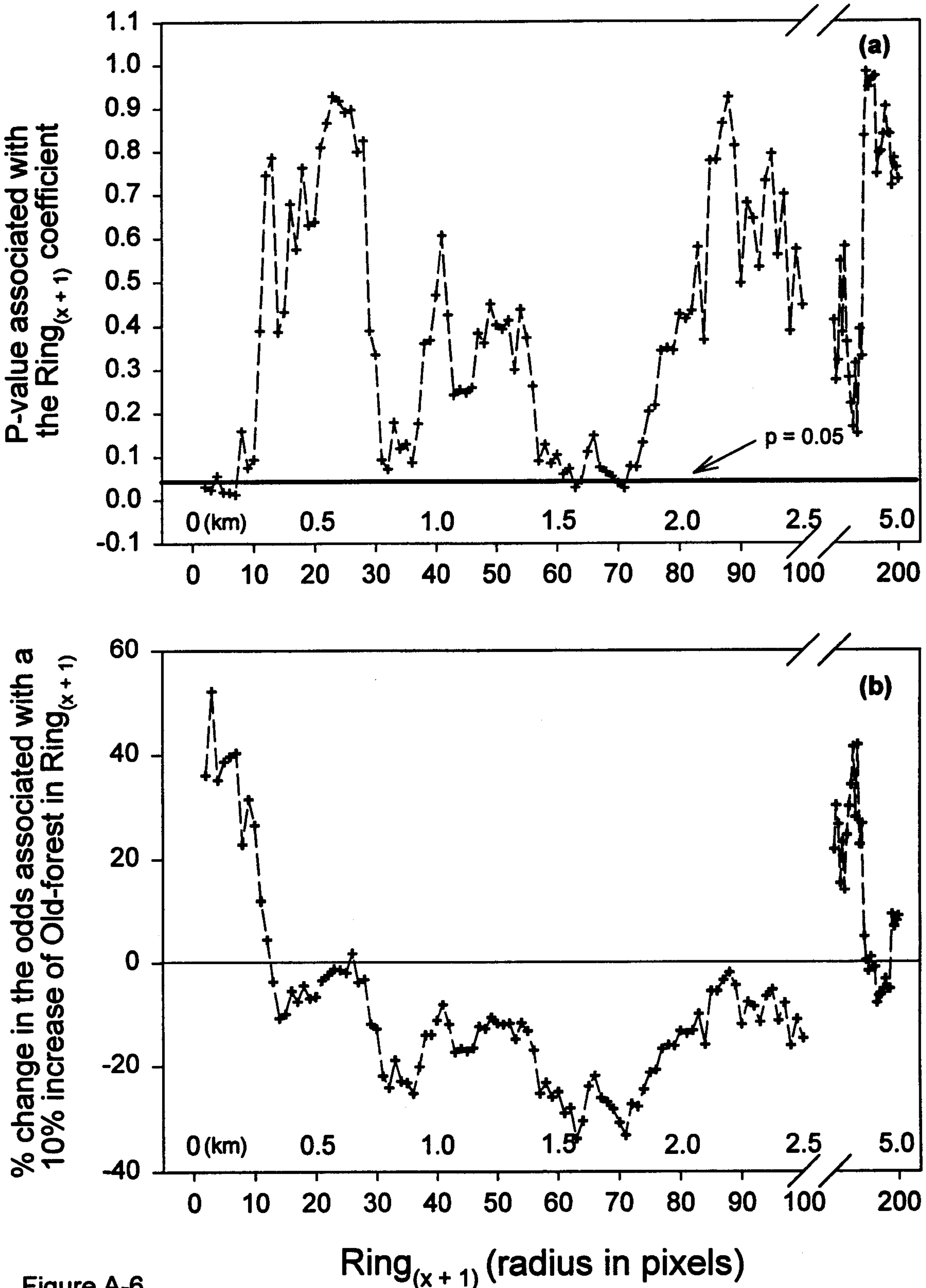
(a)
P-value associated with the Ring$_{(x+1)}$ coefficient
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
(b)
% change in the odds associated with a 10% increase of Old-forest in Ring$_{(x+1)}$
60
40
20
0
-20
-40
Ring$_{(x+1)}$ (radius in pixels)

Figure A-6.

Figure A-7. Young forest in 200 concentric circle-plots around spotted owl nest sites and totally random points. (a) percentage of young forest[19], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest (= $100[e^{(10)\beta} - 1]$). *There was less young forest in circular plots around nest sites at all scales, however, there was only significantly less ($P = 0.05$) at the center point.*

---

[19] For illustration of graph (a), only the data from every other plot size is shown.

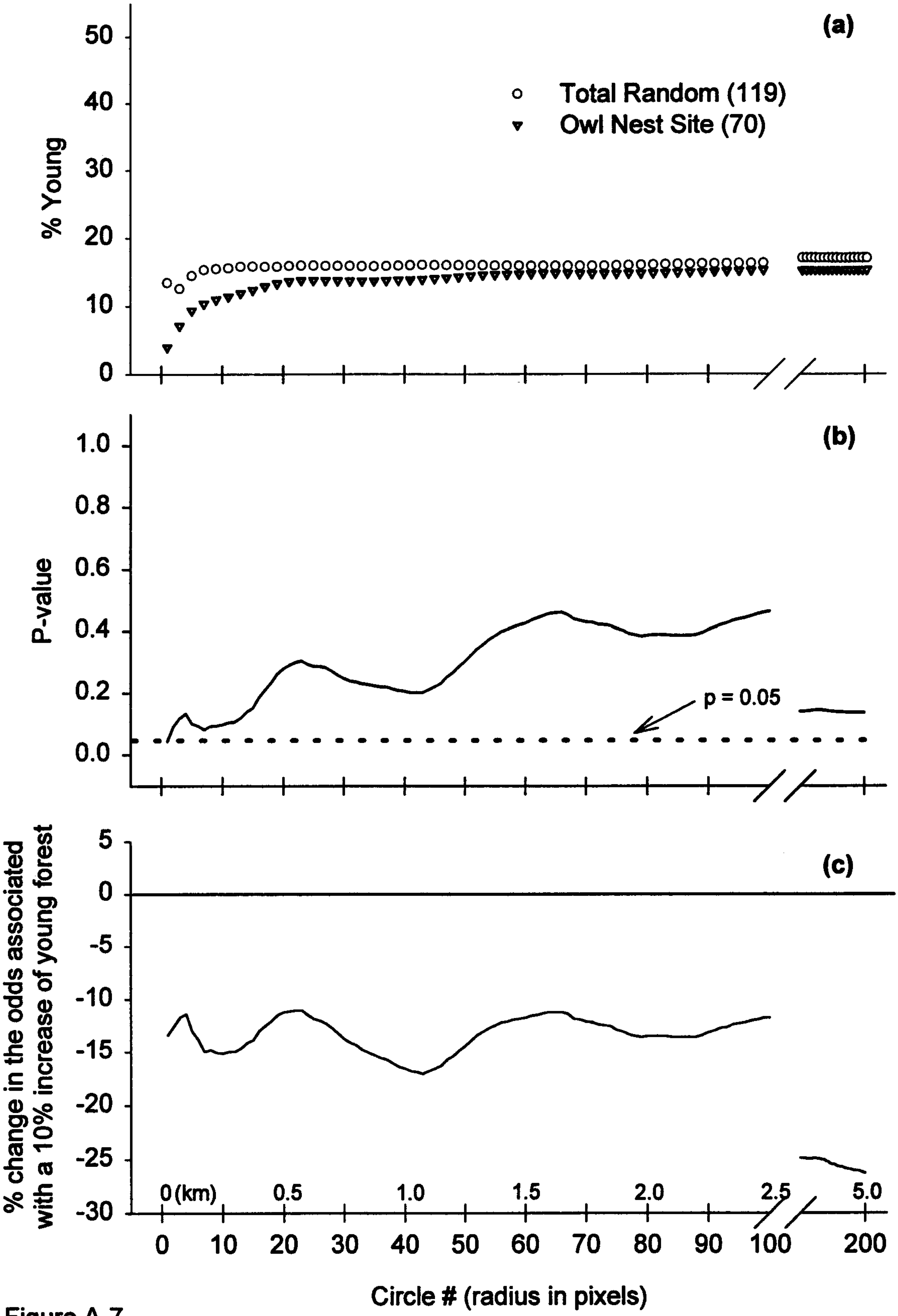
(a)
% Young
50
40
30
20
10
0
○ Total Random (119)
▼ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of young forest
5
0
-5
-10
-15
-20
-25
-30
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure A-7.

Figure A-8. Young forest in 200 concentric non-overlapping ring-plots around spotted owl nest sites and totally random points. (a) percentage of young forest[20], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$). *There were similar amounts of young forest around owl nest-sites compared to points randomly drawn from the landscape.*

---

[20] For illustration of graph (a), only the data from every other plot size is shown.

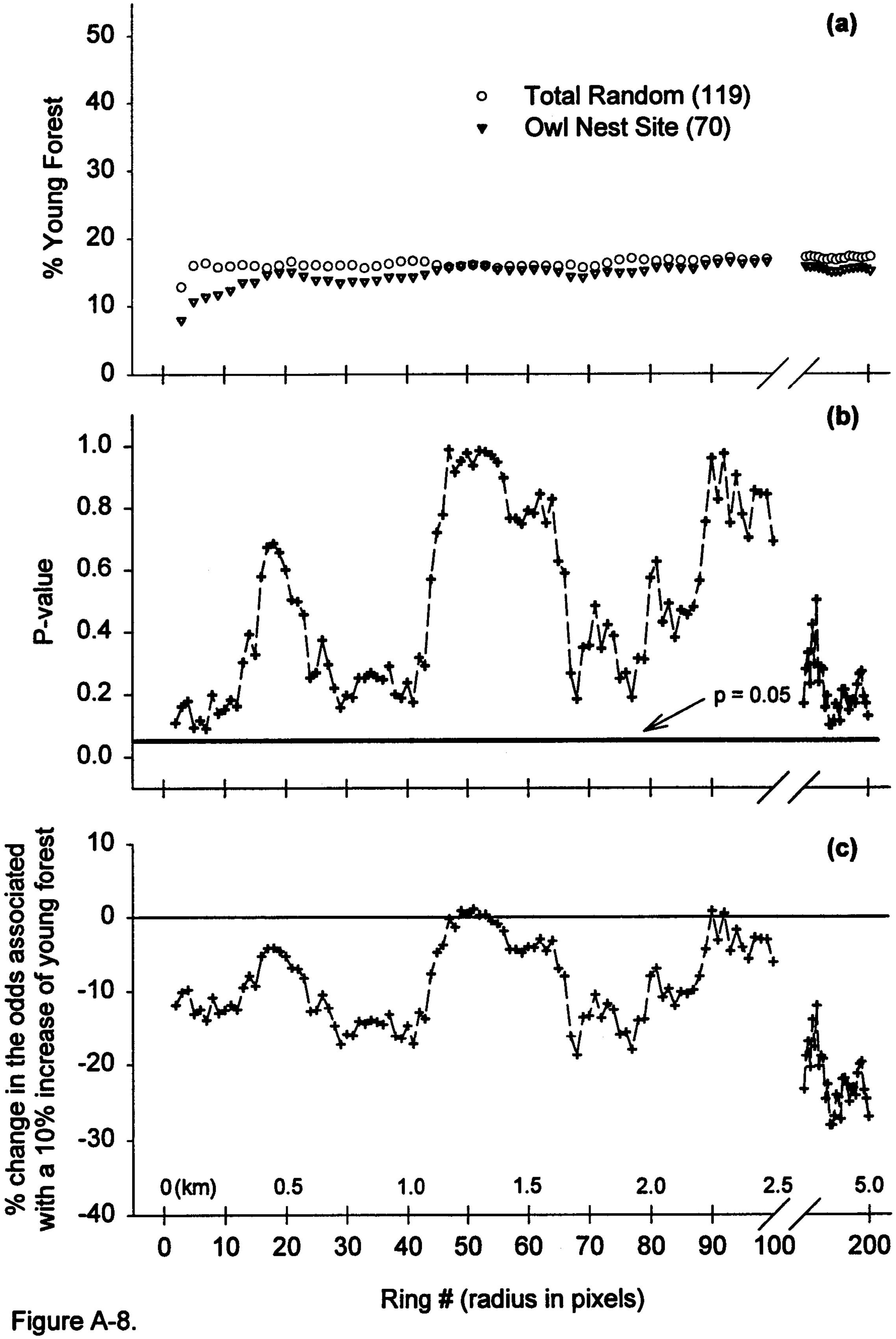
(a)
% Young Forest
50
40
30
20
10
0
○ Total Random (119)
▼ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of young forest
10
0
-10
-20
-30
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure A-8.

Figure A-9. Young forest in 200 circle + ring plots around spotted owl nest sites and totally random points. (a) p-values associated with the $\text{ring}_{(x+1)}$ coefficient, (b) extra odds associated with a 10% increase in young forest in $\text{ring}_{(x+1)}$ ($= 100[e^{(10)\beta} - 1]$). *A 10% increase in the amount of young forest had no significant effect on the additional odds that the center point was a nest site. However, increases in R45-R55, increased the additional odds ($P < 0.10$) by nearly 50%. The increases in the additional odds associated with increased amounts of young forests are at scales corresponding to the increases in the additional odds associated with decreased amounts of old-forest. Context may be given to these results by examining the % young forest profiles for circle and ring plots (Figs. A-7 and A-8 respectively). Figure A-8 shows that the amount of young forest around nest sites becomes similar to the amount around random points in rings R45 through R55.*

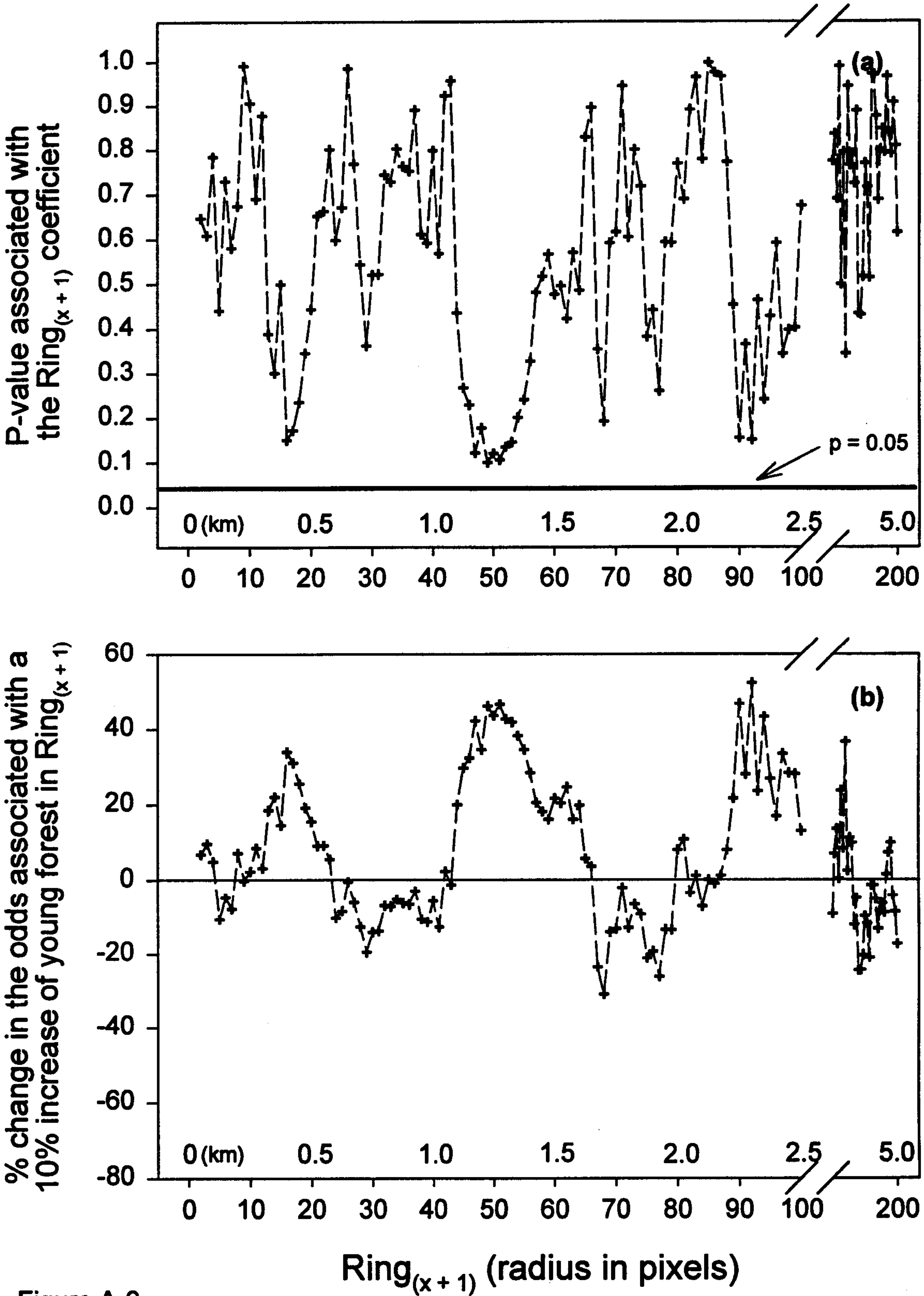
(a)
P-value associated with the $Ring_{(x+1)}$ coefficient
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
(b)
% change in the odds associated with a 10% increase of young forest in $Ring_{(x+1)}$
60
40
20
0
-20
-40
-60
-80
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
$Ring_{(x+1)}$ (radius in pixels)

Figure A-9.

Figure A-10. Young forest in 200 concentric circle-plots around spotted owl nest sites and old-forest random points. (a) percentage of young forest[21], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$). *Between the 0.01 km and 0.5 km there was more young forest around owl nest sites, however these differences were not significant ($P > 0.05$) except for the 2nd circular plot (0.06 km; $p = 0.05$). Beyond 0.5 km there was more young forest around old-forest random points, however these differences were not significant ($P > 0.05$).*

---

[21] For illustration of graph (a), only the data from every other plot size is shown.

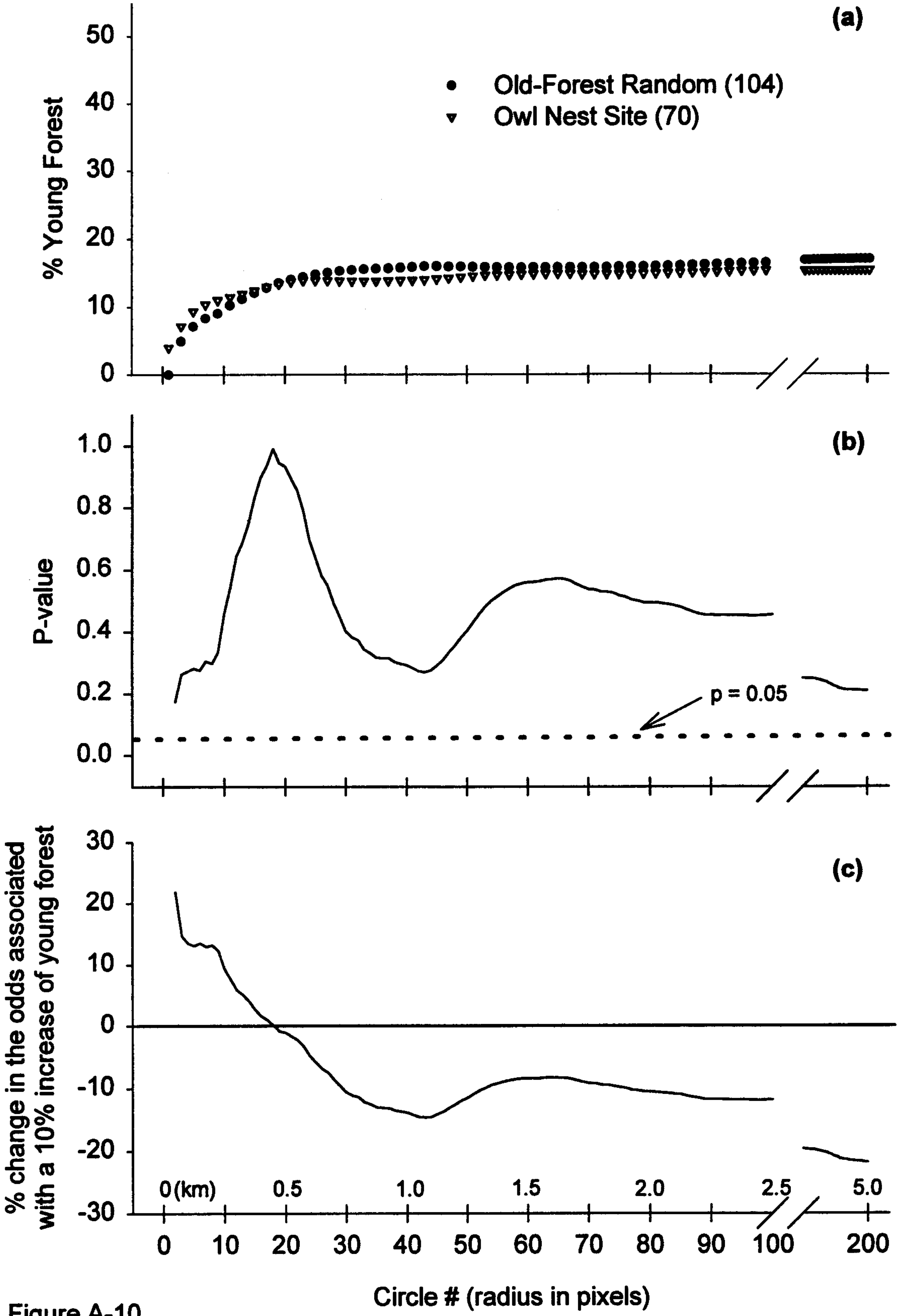
(a)
% Young Forest
50
40
30
20
10
0
● Old-Forest Random (104)
▼ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of young forest
30
20
10
0
-10
-20
-30
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure A-10.

Figure A-11. Young forest in 200 concentric non-overlapping ring-plots around spotted owl nest sites and old-forest random points. (a) percentage of young forest[22], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of young forest ($= 100[e^{(10)\beta} - 1]$). *There were no statistically significant differences ($P > 0.05$) in the amount of young forest between owl nest sites and old-forest random points. There was slightly more young forest around nest sites from 0.04 km through 0.25 km, while there was slightly less in rings with radii between 0.25 km and 1.25 k. Beyond 1.20 km amounts of young forest were essentially identical.*

---

[22] For illustration of graph (a), only the data from every other plot size is shown.

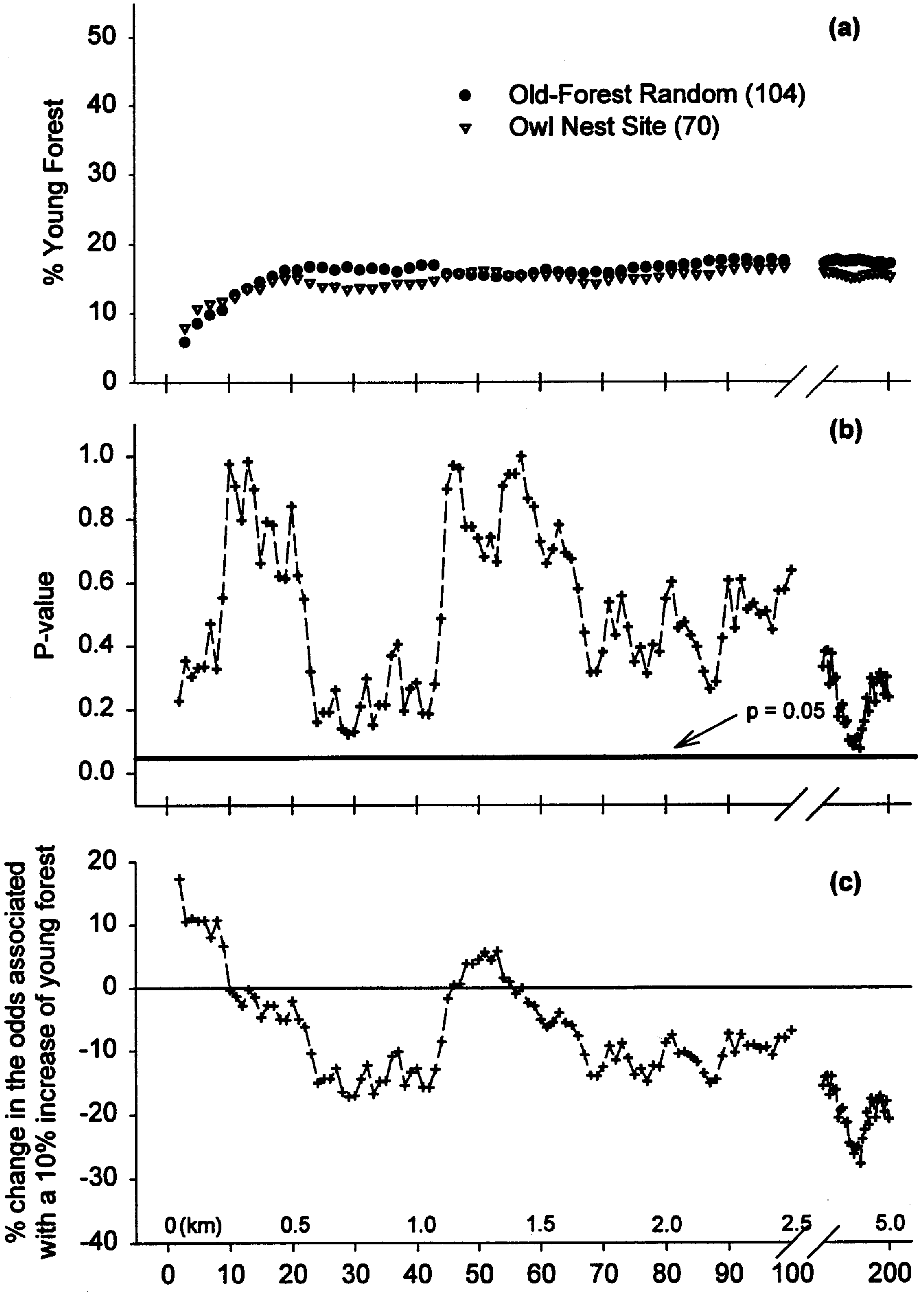
(a)
% Young Forest
50
40
30
20
10
0
● Old-Forest Random (104)
▿ Owl Nest Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of young forest
20
10
0
-10
-20
-30
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure A-11.

Figure A-12. Young forest in 200 circle+ring plots around spotted owl nest sites and old-forest random points. (a) p-values associated with the $\text{ring}_{(x+1)}$ coefficient, (b) extra odds associated with a 10% increase in young forest in $\text{ring}_{(x+1)}$ ($= 100[e^{(10)\beta} - 1]$). *A 10% increase of young habitat out to 1.10 km and beyond 1.70 km tended to decrease the odds that the center point was a nest site (but generally not significantly so). Conversely, increases in % of young habitat in rings with radii between 1.10-1.70 km tended to increase the odds that the center point was a nest site by as much as 70% (with several rings in this range being significant (P=0.05). Inspection of figures A-10 and A-11 indicate that these changes in the extra odds are associated with the scales at which the amounts of young forest in the ring plots were slightly higher (which were not significant in the ring-only analyses) around owl nests than while amounts in circle-plots were lower.*

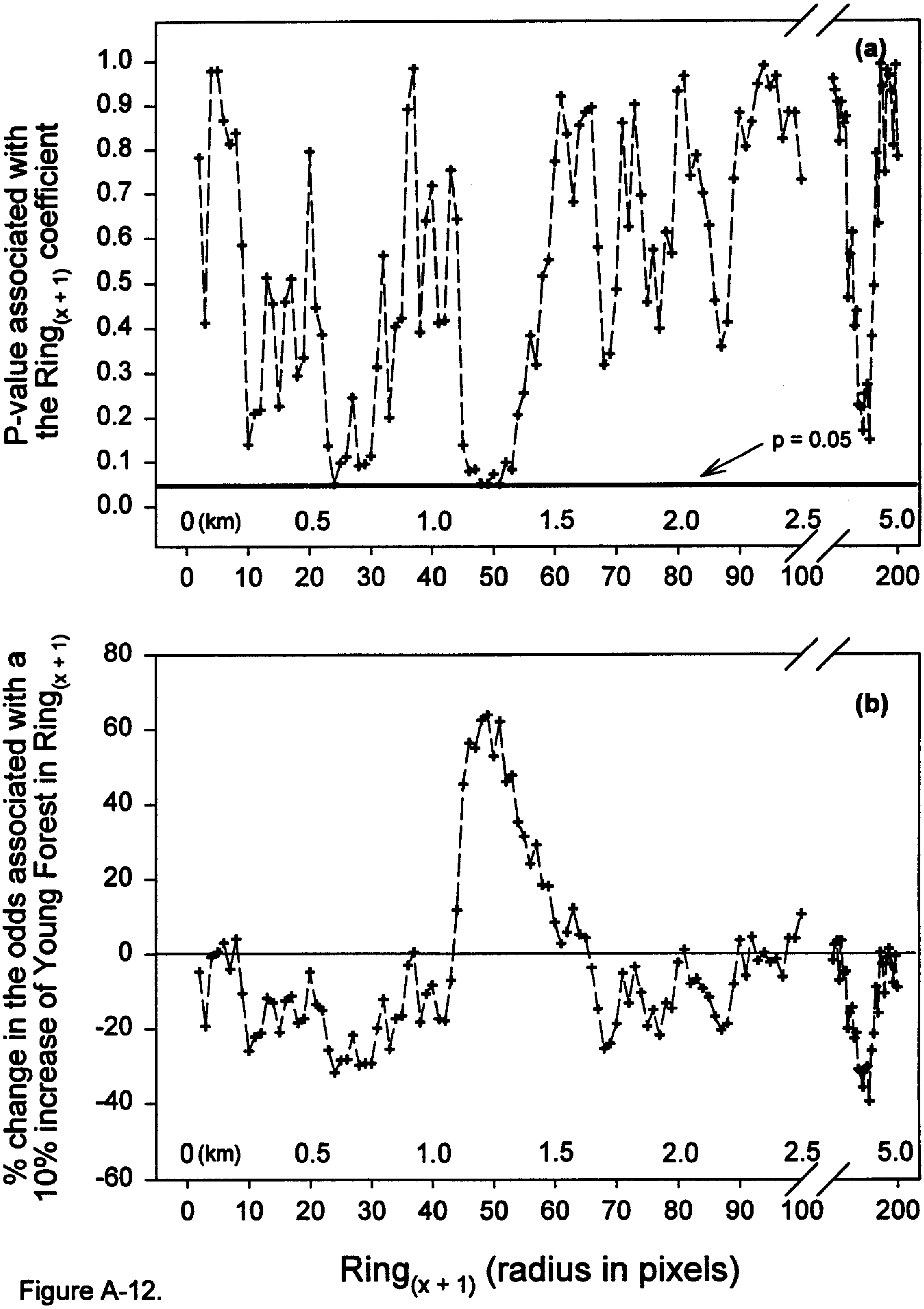
P-value associated with the Ring(x + 1) coefficient
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
(a)
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
% change in the odds associated with a 10% increase of Young Forest in Ring(x + 1)
80
60
40
20
0
-20
-40
-60
(b)
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring(x + 1) (radius in pixels)

Figure A-12.

Figure A-13. Non-habitat in 200 concentric circle-plots around spotted owl nest sites and totally random points. (a) percentage of non-habitat[23], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of non-habitat ($= 100[e^{(10)\beta} - 1]$). *There was less non-habitat around owl nest-sites at all scales and significantly less in plot sizes as large as 1.00 km.*

---

[23] For illustration of graph (a), only the data from every other plot size is shown.

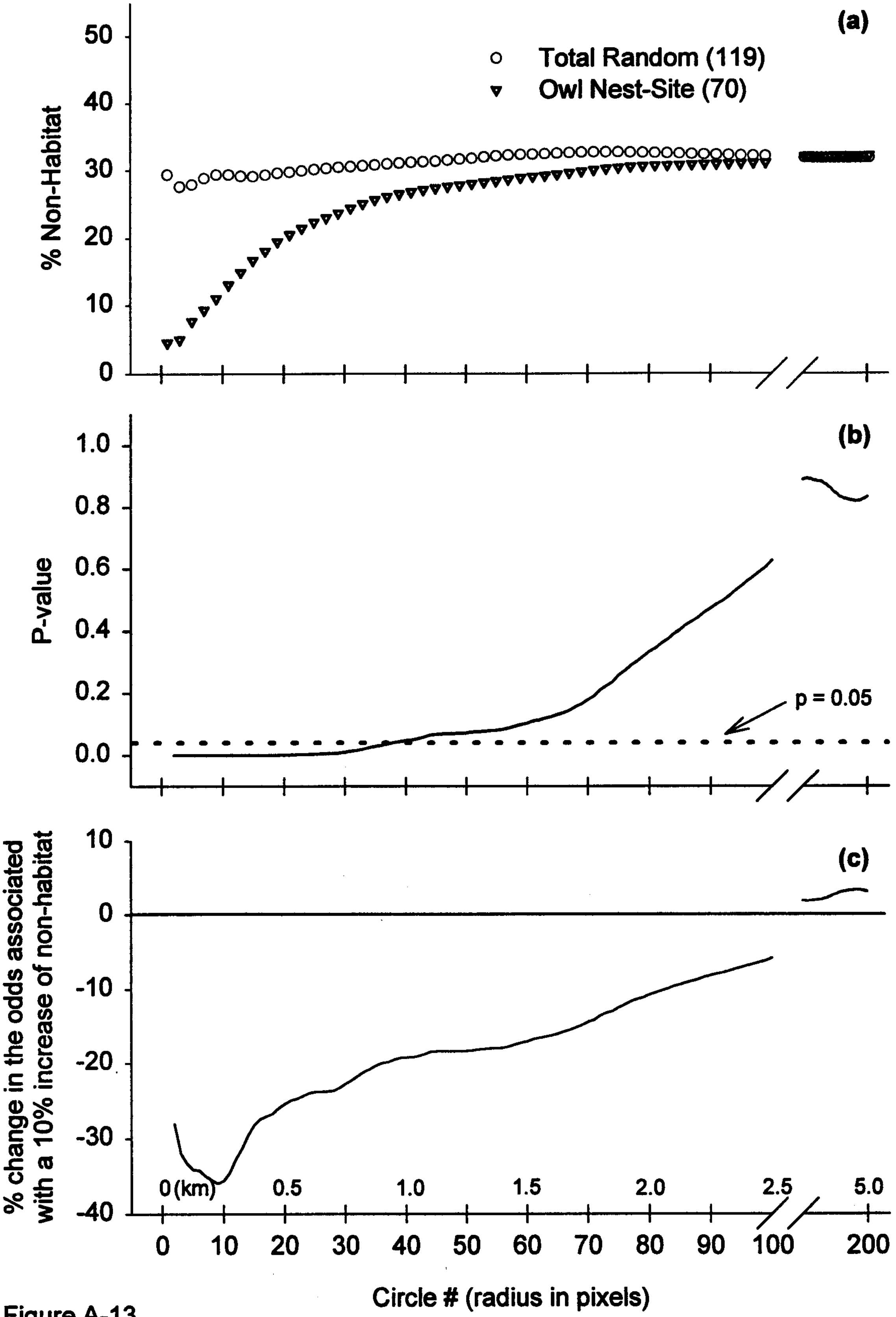
(a)
○ Total Random (119)
▼ Owl Nest-Site (70)
% Non-Habitat
50
40
30
20
10
0
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of non-habitat
10
0
-10
-20
-30
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure A-13.

Figure A-14. Non-habitat in 200 concentric non-overlapping ring-plots around spotted owl nest sites and totally random points. (a) percentage of non-habitat[24], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of non-habitat ($= 100[e^{(10)\beta} - 1]$). *There was less non-habitat around nests at all ring-plots smaller than 1.75 km in radius and significantly ($P < 0.05$) less in all ring-plots smaller than 0.45 km in radius. At scales larger than 1.86 km in radii there tended to be similar amounts.*

---

[24] For illustration of graph (a), only the data from every other plot size is shown.

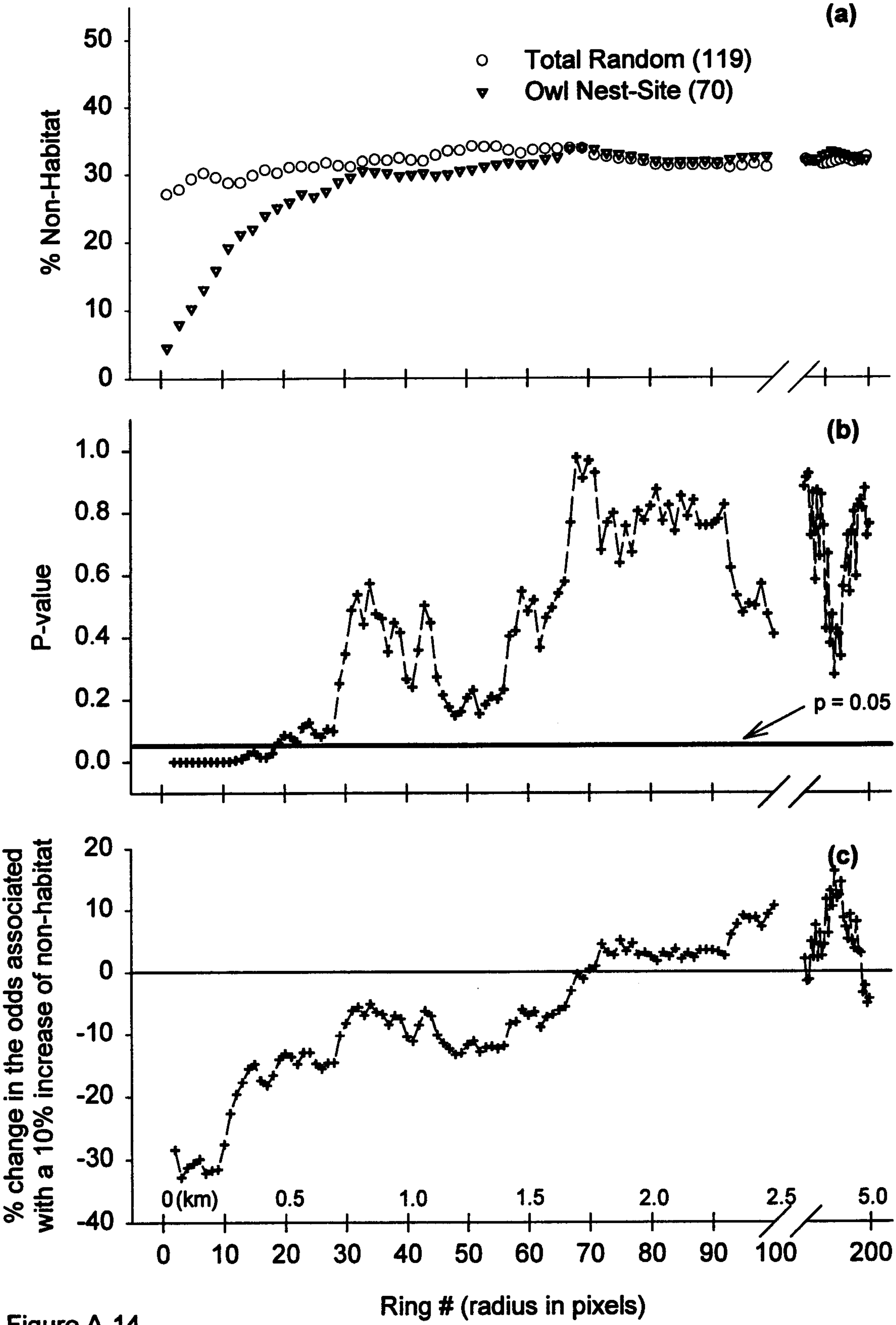
(a)
% Non-Habitat
50
40
30
20
10
0
○ Total Random (119)
▼ Owl Nest-Site (70)
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of non-habitat
20
10
0
-10
-20
-30
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure A-14.

Figure A-15. Non-habitat in 200 circle + ring plots around spotted owl nest sites and totally random points. (a) p-values associated with the $\text{ring}_{(x+1)}$ coefficient, (b) extra odds associated with a 10% increase in non-habitat in $\text{ring}_{(x+1)}$ $(= 100[e^{(10)\beta} - 1])$. *After accounting for the amount of non-habitat in the central portions (circles) of plots, a 10% increase of non-habitat increased the additional odds that the center point was a nest site, with significant increases of up to 100% in most rings beyond 0.25 km radius. Figures A-13 and A-14 indicate that the points at which the amount of non-habitat becomes slightly higher around nest sites correspond to the points at which the ring coefficients become most significant. Figure A-14 also places the "significance" of these rings into context (i.e. not very meaningful).*

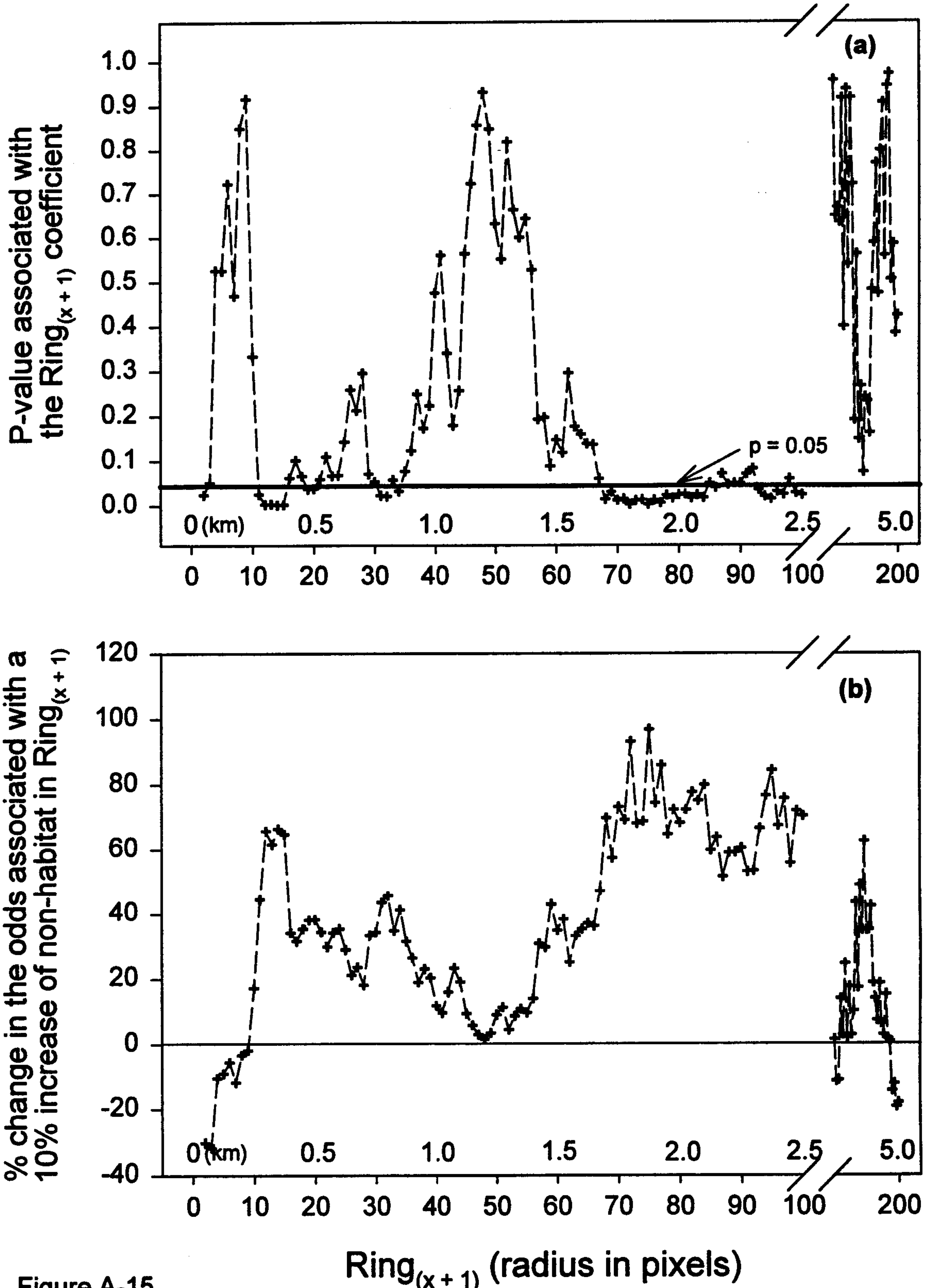
(a)
P-value associated with the $\text{Ring}_{(x+1)}$ coefficient
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
(b)
% change in the odds associated with a 10% increase of non-habitat in $\text{Ring}_{(x+1)}$
120
100
80
60
40
20
0
-20
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
$\text{Ring}_{(x+1)}$ (radius in pixels)

Figure A-15.

Figure A-16. Non-habitat in 200 concentric circle-plots around spotted owl nest sites and old-forest random points. (a) percentage of non-habitat[25], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of non-habitat (= $100[e^{(10)\beta} - 1]$). *There was less non-habitat around owl nest sites between out to 1.75 km and slightly more (non-significantly $P > 0.05$).*

---

[25] For illustration of graph (a), only the data from every other plot size is shown.

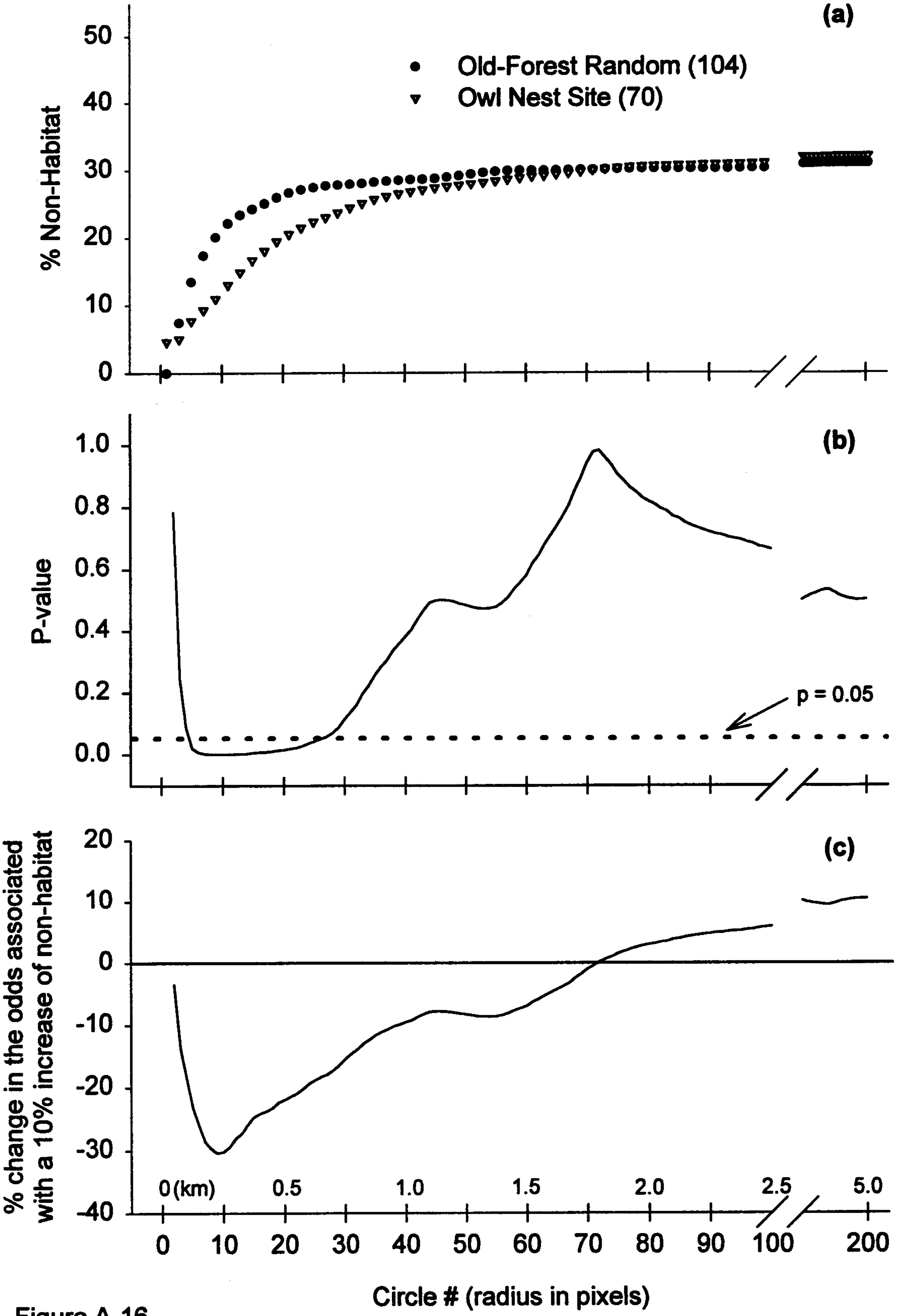
(a)
● Old-Forest Random (104)
▼ Owl Nest Site (70)
% Non-Habitat
50
40
30
20
10
0
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of non-habitat
20
10
0
-10
-20
-30
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Circle # (radius in pixels)

Figure A-16.

Figure A-17. Non-habitat in 200 concentric non-overlapping ring-plots around spotted owl nest sites and old-forest random points. (a) percentage of non-habitat[26], (b) p-values for logistic regressions of nest sites vs. random points, (c) % change in the odds associated with a 10% increase of non-habitat (= $100[e^{(10)\beta} - 1]$). *There was less non-habitat around nest sites out to 0.80 km with significantly ($P < 0.05$) less out to 0.40 km. Amounts of non-habitat did not differ significantly in all other plot sizes, however, beyond 1.43 km there were consistently higher amounts of non-habitat.*

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[26] For illustration of graph (a), only the data from every other plot size is shown.

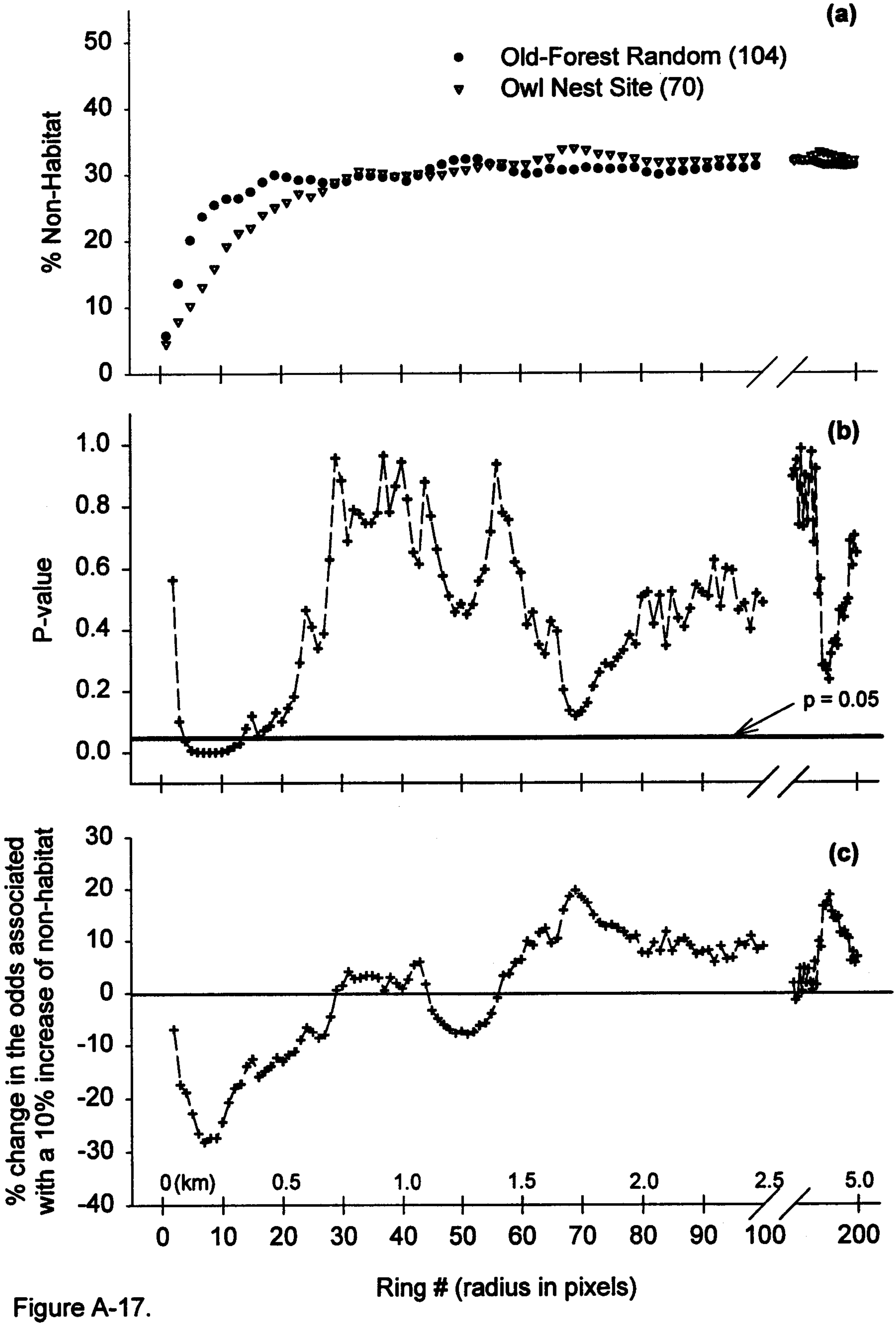
(a)
● Old-Forest Random (104)
▾ Owl Nest Site (70)
% Non-Habitat
50
40
30
20
10
0
(b)
P-value
1.0
0.8
0.6
0.4
0.2
0.0
p = 0.05
(c)
% change in the odds associated with a 10% increase of non-habitat
30
20
10
0
-10
-20
-30
-40
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring # (radius in pixels)

Figure A-17.

Figure A-18. Non-habitat in 200 circle+ring plots around spotted owl nest sites and old-forest random points. (a) p-values associated with the $\text{ring}_{(x+1)}$ coefficient, (b) extra odds associated with a 10% increase in non-habitat in $\text{ring}_{(x+1)}$ ($= 100[e^{(10)\beta} - 1]$). *A 10% increase of non-habitat in rings out to 0.20 km significantly ($P < 0.05$) decreased the odds that the center point was a nest site by as much as 39%. In contrast, increases in the amount of non-habitat beyond that distance tended to increase them, and some significantly so ($P < 0.05$), by as much as 90%. Once again, inspection of figures A-16 and A-17 indicate that these scales generally correspond to those at which the amount of non-habitat is slightly higher (not significantly so according to the ring-only analyses) in rings around nest sites than around old-forest random points.*

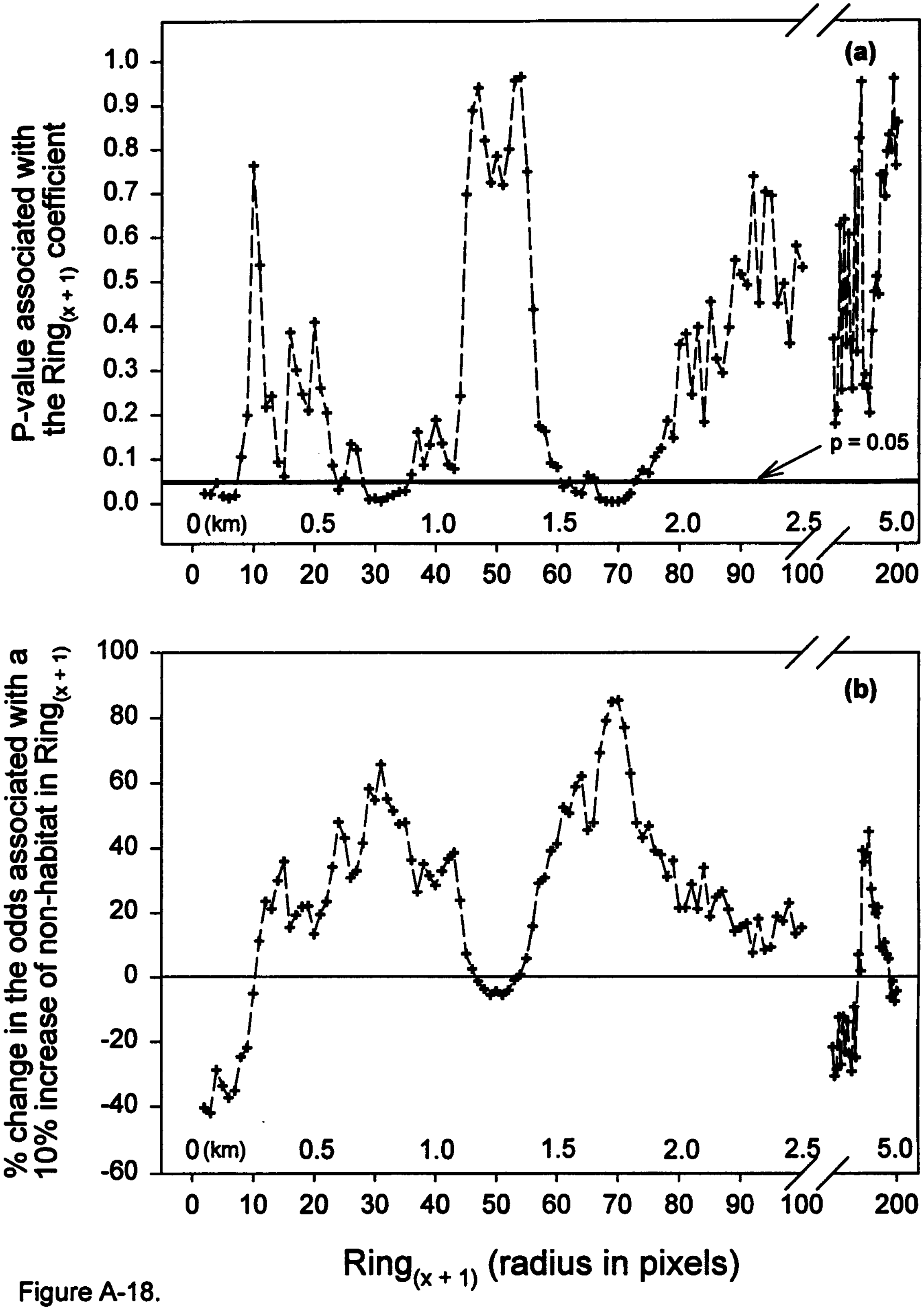
(a)
P-value associated with the Ring$_{(x+1)}$ coefficient
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
p = 0.05
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
(b)
% change in the odds associated with a 10% increase of non-habitat in Ring$_{(x+1)}$
100
80
60
40
20
0
-20
-40
-60
0 (km)
0.5
1.0
1.5
2.0
2.5
5.0
0
10
20
30
40
50
60
70
80
90
100
200
Ring$_{(x+1)}$ (radius in pixels)

Figure A-18.