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Ecological integrity of remnant montane forests along an urban gradient in the Sierra Nevada

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Abstract

Urban development typically has extensive and intensive effects on native ecosystems, including vegetation communities and their associated biota. Increasingly, urban planning strives to retain elements of native ecosystems to meet multiple social and ecological objectives. The ecological integrity of native forests in an urbanizing landscape is challenged by a myriad of impacts, such as forest management and invasive species. Environmental protection efforts in the Lake Tahoe basin, spanning the California/Nevada border in the Sierra Nevada mountains, over the past half century have resulted in the retention of thousands of parcels of remnant native forest located throughout the urbanizing landscape. The basin landscape provides an opportunity to evaluate the effects of land development on the composition and structure of remnant native forests along a gradient of urbanization. We sampled 118 sites located in remnant forests in the lower montane zone surrounded by 0–70% development. We also sampled forest structure in the landscape surrounding 75 of these sites to evaluate the contribution of remnant forests to the retention of native forest elements in the larger landscape. We characterized plant species composition and cover, vertical structure, and the density of trees, snags, and logs, as well as levels of ground disturbance and human activity. We found that remnant native forests retained much of their compositional and structural character along the development gradient, including large tree density, total canopy cover, and plant species richness. Notable exceptions were reductions in the density and decay stage of snags and logs, and the density of understory trees. We also observed increases in the richness and cover of herb and grass species and increases in the number of exotic plant species. In contrast, structural complexity was reduced in the landscape surrounding forest remnants in all measures except large tree density. We conclude that remnant native forests contribute significantly to maintaining native species in an urbanizing landscape, and that land conservation practices have an important role to play in protecting native forest ecosystems.

Keywords: Exotic plant species; Lake Tahoe; Montane forest structure; Sierra Nevada; Snags and logs; Urban gradient

1. Introduction

Urban development generally has ecologically significant and lasting effects on native ecosystems, including vegetation communities and their associated biota (McKinney, 2002). Increasingly, urban planning strives to retain elements of native ecosystems and their associated functions to enhance aesthetics, provide recreation opportunities, contribute to the retention of biological diversity in the regional landscape, and maintain valued ecosystem services, such as insect control, flood control, and pollination (Kremen and Ostfeld, 2005). The dynamic nature of native forest communities makes it challenging to achieve the variety of social, ecological, and economic objectives that commonly drive their retention (Folke et al., 2005). Forest ecosystems are particularly vulnerable to loss of ecological integrity given the intrinsic complexity of their structure and function (e.g., World Commission on Forests and Sustainable Development, 1999; Karnosky et al., 2001). As per Karr and Dudley (1981), we define ecological integrity as the ability of an ecological system to support and maintain a community of organisms that has species composition, diversity, and functional organization comparable to those of

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natural habitats within a region. An ecological system has integrity when its dominant ecological characteristics (e.g., elements of composition, structure, function, and ecological processes) occur within their natural ranges of variation (Parrish et al., 2003).

Vertical structure and species composition are key elements of ecological integrity in native conifer forests (e.g., Yongblood et al., 2004), and, although readily measured and directly managed, they can be difficult to retain in urban settings (Sanders, 1984). For example, a 48-year study of changes in forest canopy in a 16-ha remnant forest patch in the New York Botanical Garden showed that overstory canopy composition had been significantly altered by changes in disturbance regime (Rudnicky and McDonnell, 1989). The authors concluded that urban stresses, such as trampling, arson, and vandalism created edges and open areas where more light could penetrate, favoring the establishment of early-successional, shade-intolerant species. Human activities, such as construction, trenching, paving, sewage effluent disposal, insecticidal spraying of trees for mosquito control, and road de-icing, can promote disease by injuring trees (Ferrell, 1996). Soil compaction from various human activities can also degrade tree health by reducing leaf growth and changing root morphology (Lambers et al., 1998).

Urbanization is commonly accompanied by an increase in the number of non-native plant species and a decrease in the richness of the native flora (Bagnall, 1979; Airola and Buchholz, 1984; Hobbs, 1988; Rudnicky and McDonnell, 1989; Kowarik, 1995; Hill et al., 2002). Native vegetation is often reduced in diversity through trampling, soil compaction, erosion, pruning, mowing, pollution, and competition with exotic species (Gilbert, 1991; Adams, 1994; McKinney, 2002). Increases in non-native species are functions of an increased proportion of disturbed soil, which provides opportunities for weedy non-native plants, and propagation of non-native horticultural plants (Kowarik, 1995). Declines in native species richness can have far-reaching effects on ecosystem function and resilience in the face of changing environmental conditions (e.g., Hooper et al., 2005; Hector and Baqchi, 2007).

In addition to intrinsic changes in forest conditions, an inevitable consequence of urbanization is habitat fragmentation and increased isolation. Habitat loss and fragmentation reduces population sizes of habitat specialists restricted to fragments, and small population sizes can put populations at risk of extirpation through demographic and environmental stochasticity and disruption of metapopulation dynamics (Debinski and Holt, 1998). Concomitantly, increased isolation of remaining habitat can decrease colonization of native species, particularly short-distance dispersers (Eriksson and Ehrlen, 2001; Jacquemyn et al., 2001; but see Yaacobi et al., 2007). Further, habitat patches have increased vulnerability to invasion by exotic species or opportunistic natives and changes in microclimate, particularly increasing wind and temperature as the amount of edge increases (Saunders et al., 1991).

Despite high rates of human population growth and concomitant urban expansion in some parts of the western United States (Theobald, 2005), research directed at urban ecosystems in this region is rare (but see Soule et al., 1992; Grimm et al., 2003; Alberti and Marzluff, 2004; Hope et al., 2006). The Sierra Nevada in California is experiencing a rapidly expanding resident population, predicted to triple over the 50-year period of 1990–2040 (Duane, 1996). The Lake Tahoe basin, located in the central Sierra Nevada, is under increasing pressure from urbanization and habitat fragmentation due to tourism, recreation, and residential populations. Private and public land-acquisition programs have curbed development by setting aside thousands of parcels (often <1 ha), interspersed in urbanizing areas, to remain undeveloped. These parcels are thought to contribute to biological diversity and other important ecosystem functions (Elliot-Fisk et al., 1996); however, a limited number and scope of investigations have probed these assumptions to enhance our understanding of the ecological integrity and vulnerability of remnant forests in this urbanizing landscape (see McBride and Jacobs, 1979, 1986). This unique landscape provides a valuable opportunity to study the dynamics of remnant native communities in an urbanizing setting.

The objectives of this study were twofold: (1) to determine how the composition, structure, and function of native forests change along a gradient of urbanization, and (2) to compare vegetation in remnant forests to that of the adjacent, surrounding landscape to provide a context for interpreting the contribution of remnant forests to meeting management objectives. We expected that, as urbanization increased, remnant forests would have reduced ground cover, lower tree density, greater prevalence of conifer disease symptoms, lower species richness, and a greater number of exotic species. We also expected conditions in the surrounding landscape to exhibit the same types of changes as forest remnants but to a greater degree in areas with higher levels of urban development, which may lack remnant forest.

2. Methods

2.1. Study area

The Lake Tahoe basin lies high in the central Sierra Nevada, flanked by the Sierra Nevada in California to the west and the Carson Range in Nevada to the east (38.90° N and 120.00° W). The centerpiece of the basin is Lake Tahoe, with a surface area of 49,000 ha, and its surrounding watershed, which covers 82,000 ha (Barbour et al., 2002) and ranges in elevation from 1900 m a.s.l. at lake level to 3050 m at the highest peak (Elliot-Fisk et al., 1996). A strong precipitation gradient exists from west to east, such that the Tahoe basin encompasses two very different climate regimes. Average annual precipitation on the northeast shore is about half that on the southwest shore (Kittel, 1998). Two-thirds of the annual precipitation falls from December to March, more than 80% of which falls as snow. The winter mean daily minimum temperature at lake elevation is about -6 °C, while the mean summer daily temperature exceeds 30 °C (Manley et al., 2000).

The basin contains three main vegetated life zones: lower montane (lake level to 2200 m a.s.l.), upper montane (2200–

2600 m a.s.l.), and subalpine (>2600 m a.s.l.). This project was restricted to elevations (1920–2134 m) within the lower montane zone because that zone contained approximately 95% of the urban area in the basin (Tahoe Regional Planning Agency, 2002). The most common lower montane forest types are Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), mixed-conifer, and white fir (*Abies concolor* [Gordon & Glend.] Lindley; Manley et al., 2000). In addition, forest dominated by lodgepole pine (*Pinus contorta* Loudon) is found in moist habitats throughout the basin and a mix of alder (*Alnus* spp.), willow (*Salix* spp.), and aspen (*Populus tremuloides* Michaux) is common in riparian areas.

2.2. Study design

We sampled sites along an urban–rural gradient (McDonnell and Pickett, 1990). Most studies of the effects of urbanization sample discrete levels of urban development (e.g., urban vs. rural; Baxter et al., 1999; Theobald, 2004) or along transects radiating away from urban centers (e.g., Lovett et al., 2000). We sampled a gradient of urban development by creating a GIS-based urban development model (Manley et al., 2006). Any area that had a land-use type that removed native vegetation was considered developed. Land-use types (e.g., single family dwelling, hotel/motel, service station) were derived from county parcel maps. We calculated the average percent of the parcel developed for each of the 90 different land-use types occurring in the basin, and then randomly allocated that average percent development to 3-m × 3-m pixels within each grid cell (30-m × 30-m) within each parcel. We combined this data layer with roads and trails; roads and trails were converted to a grid with a pixel size of 3 m × 3 m and added to the development associated with 30 m × 30 m pixel. Finally, we used a GIS moving window function to assign percent developed within various radii to each 30-m × 30-m grid cell. We used the 300-m radius circle as our sampling frame and each grid cell as sample unit.

We selected 118 sample sites along the development gradient. We required sites to be ≥0.5 km apart for independence, consist of ≥0.1 ha of native forest to accommodate sampling, have a <45% slope to reduce variance among sites, and have >10% forest cover. Sites were randomly stratified by 20% development classes within each of the three primary development areas in the basin (north, west, and south sides of the basin). Eleven sites selected were in old-growth forest, identified by Barbour et al. (2002), all of which were located on the west side of the basin (the only place they exist).

2.3. Vegetation data collection

We collected field data in 2003 and 2004. At the center of each sample site, we used three nested circular plots to describe forest structure based on the response design of the Forest Inventory and Analysis program (2002; Fig. 1). We located three nested plots at the center of the array: a 0.017-ha circular microplot centered within a 0.1-ha circular subplot and a 1-ha circular macroplot, which encompassed the all subplots. Three

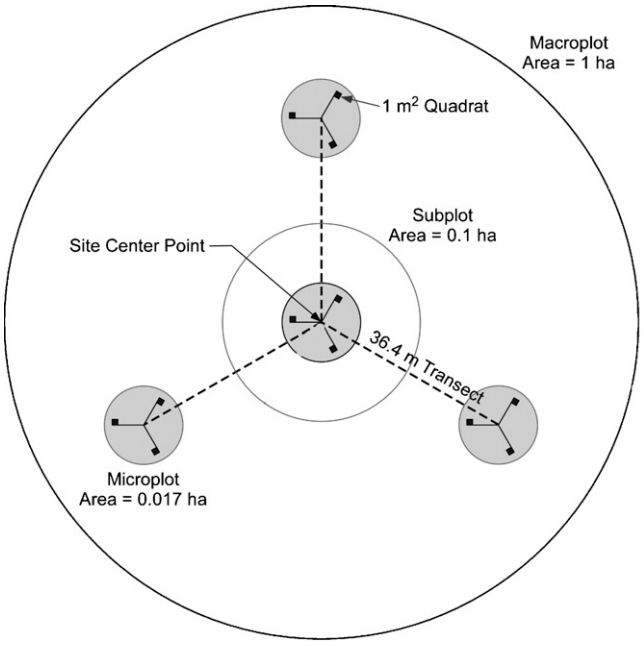

Fig. 1. Layout of subplots, quadrats, and transects employed at the center point of each sample site in the Lake Tahoe basin, 2003–2004.

additional microplots were established 36.4 m away at 0°, 120°, and 240°. We recorded all trees and snags ≥12.5 cm diameter at breast height (dbh) in each microplot; only trees >28 cm and snags ≥12.5 cm dbh were recorded in each subplot; and only trees >61 cm and snags >30.5 cm dbh were recorded in the macroplot. Each tree was characterized as follows: species, height (using a clinometer), dbh, decay class (snags; Thomas et al., 1979), and presence of decadence or disease (cavities >15 cm in diameter, broken top, broken limb >30 cm in diameter, split top, dead top, loose bark, mistletoe, thin canopy, light foliar color, leaf necroses, frass, sap exudation, conks). We also counted cut tree stumps ≥10 cm diameter within each subplot. Percent canopy closure (per Jennings et al., 1999) was estimated with a moosehorn device (Garrison, 1949) in each cardinal direction around the circumference of each subplot.

We also characterized plant species composition and cover (per Jennings et al., 1999) within microplots by visually estimating percent cover of trees, shrubs, and non-native plant species. The composition and cover of herbs was estimated visually to the nearest 1% within each of three 1-m^2 quadrats per microplot (12 total per site). We also searched each microplot for 15 min to record any additional plant species present at the site. Ornamental plants were not identified to species, but lumped into one of three categories: ornamental herb, shrub, or tree.

We used three 30-m line-intercept transects to characterize vertical structure and downed woody material or "logs"; the first transect was placed at a random azimuth and the remaining two were placed 120° in either direction. Along these transects, we recorded the following information: (1) at 3-m intervals (n = 30 total), the presence of all plant species within 5-m height intervals; (2) length, diameter at each end, and decay class (Maser et al., 1979) of each log ≥10 cm diameter at the large end that intersected the transect.

In addition to sampling at the center of each site, at 75 of the 118 sites we also sampled vegetation structure at a point 200 m away from the center of the site in each of the four cardinal directions (precise locations depended on access). Sites were randomly selected within development strata to be representative of the development gradient and all basin orientations. These 300 additional sites were not limited to remnant forest; thus, they represented the condition of the surrounding landscape. These data were used to describe how development affects forest structure outside of remnant native forest stands and to compare conditions between remnant forest stands and the surrounding landscape. At the surrounding-landscape sites, we limited sampling to two nested plots (micro and sub) where we recorded tree and snag data and vegetative cover using the same methodology as at the center of the site, canopy closure at each of the four cardinal directions around the subplot using a spherical densiometer, and data on downed woody material along three 30-m transects (as per the center plot, except that we recorded only logs $\geq$28 cm at the large end).

2.4. Development and human activity

We had the option of representing development at a range of scales around each sample site. Land development initially was calculated at multiple scales (100, 300, 500, and 1000-m radii) using the GIS buffering functions. All four scales of development were highly correlated and preliminary analyses showed that choice of scale did not affect relationships between development and various vegetation measures (e.g., species richness, tree density). Therefore, development within a 300-m radius (same scale used for site selection) was used for all analyses.

Human activity was characterized within a square 4-ha area centered on each site. Approximately 1 km of walking routes and five count stations were used to characterize the type and frequency of use. In sites too small to accommodate the full survey route, we restricted sampling to the undeveloped parcel and reduced sample effort while maintaining the equivalent effort per unit area. Observers walked routes at a fixed pace and stopped at the count stations for 3 min, noting the number of people, dogs (on and off leash), and vehicles encountered and the total duration of the survey. Each site was surveyed once per week, stratified by day of the week (weekday and weekend/holiday), time of the day (dawn to mid-day, mid-day to evening), and month (May through September).

2.5. Data analysis

We used Canonical Correspondence Analysis (CCA) to evaluate the relative influence of anthropogenic effects and other environmental effects on plant community composition and cover. CCA is a direct gradient analysis relating species composition to selected environmental variables (McCune and Grace, 2002) that is well documented in the ecological literature (Borcard et al., 1992; Jean and Bouchard, 1993; Okland and Eilertsen, 1994; Birks, 1996; Ohmann and Spies, 1998). The species matrix contained the mean percent cover for each of the 69 plant species occurring at >5% of sites (per McCune and Grace, 2002), based on microplot data for trees and shrubs and quadrat data for herbs. The variable matrix contained five anthropogenic variables and eight environmental variables (Appendix A). Three separate CCA ordinations were preformed: (1) CCA with all environmental (E) and anthropogenic (H, for human) variables and no covariates (H∪E), which provided the total inertia (similar to variance) of the dataset; (2) CCA of E with H as covariates (E|H), which removed the effects of the anthropogenic variables from the effects of the environmental variables; and (3) CCA of H with E as covariates (H|E), which removed the effects of the environmental variables from the anthropogenic variables (per Palmer, 2005). From these analyses, we were able to extract the following values (per Palmer, 2005): (1) total variation explained by E|H, obtained from the sum of all canonical eigenvalues from CCA of E|H; (2) total variation explained by H|E, obtained from the sum of all canonical eigenvalues from CCA of H|E; (3) intersection of H and E (H∩E) = H∪E − E|H − H|E, using the sum of all canonical eigenvalues; and (4) unexplained variation, obtained from total inertia minus the sum of all canonical eigenvalues from the CCA of H∪E. These values were then divided by the total inertia and multiplied by 100 to get the percent of variance explained by each combination of variables (per Palmer, 2005). We used default settings in Canoco 4.5 and CanoDraw 4.0 for windows (ter Braak and Smilauer, 2002).

We derived multiple measures of forest structure, composition, and diversity (Appendix A) to evaluate the effects of development on remnant forests and the surrounding landscape. Development was grouped into three classes for some comparisons: low (<10%), moderate (10–40%), and high (>40%). Tree densities were analyzed in three diameter classes: small (12.5–28.0 cm dbh), medium (>28.0–61.0 cm dbh), and large (>61.0 cm dbh). Snags were analyzed in two diameter classes: small (12.5–30.5 cm) and large (>30.5 cm).

We used the attribute estimation techniques forwarded by Waddell (2002) to calculate log density. We first calculated the volume of each log:

$$V_{\mathrm{m}} = \frac{(\pi/8)(d_{\mathrm{S}}^2 + d_{\mathrm{L}}^2)l}{10,000}$$

where V_{m} is volume (m^3), d_{S} is small-end diameter (cm), d_{L} is large-end diameter (cm), and l the log length (m). For regression analyses, we then calculated log density (m^3/ha) per site:

$$D_{\mathrm{m3/ha}} = \sum^{i} \left(\frac{\pi}{2L}\right)\left(\frac{V_{\mathrm{m}i}}{l_i}\right)10,000$$

where L is the total length of the transects, $V_{\mathrm{m}i}$ is the volume of a log i, and l is the length of log i.

Height class diversity was calculated as the number of 5-m height classes in which vegetation occurred across the 30 transect sample points. We calculated dominance within each life form (tree, shrub, herb/grass) using the Berger–Parker index (d), where $d = N_{\max}/\Sigma N$ and N is the cover value for each species (Berger and Parker, 1970; May, 1975; Magurran, 2004).

We also obtained a number of environmental variables from publicly available GIS data layers, including slope, aspect, elevation, precipitation, wetness (measure of site moisture), heat load index (measure of heat exposure), and last snow-melt date (Appendix A).

We used simple linear regression (SAS Institute Inc., 2002) to evaluate forest conditions in remnant forests relative to percent urban development. We used analysis of covariance (ANCOVA) to determine how the structure of surrounding landscapes changed with development and relative to changes in remnant forests. Percent development was treated as a covariate and site clusters were treated as a random effect, thereby accounting for potential spatial autocorrelation within landscape and remnant forest site clusters (PROC MIXED, SAS 9.1). Dependent variables were transformed as needed to meet statistical assumptions of regression analysis (see Appendix A; Sokal and Rohlf, 1994). In the rare occasions where extreme outliers (>3 standard deviations away from the mean) existed, they were removed from the analyses.

3. Results

We recorded 330 native plant species across the 118 sample sites. Thirteen percent ($n = 43$) of the species were common (occurred in >20% of sample sites), 22.7% ($n = 75$) were infrequent (occurred in 5 to ≤20% of sample sites), and 64.2% ($n = 212$) were rare (occurred in ≤5% of sample sites). In addition, we encountered 40 naturalized exotic species (8 perennial grasses, 4 annual grasses, 11 annual herbs, 4 biennial herbs, 10 perennial herbs, 1 shrub, and 2 trees).

3.1. Community ordination and variance partitioning

The CCA with both sets of variables included explained 16.1% of the variation in plant species composition and cover (Table 1a). Ordination Axis 1 was negatively correlated with soil wetness ($r = -0.85$), no-snow date ($r = -0.81$), and precipitation ($r = -0.68$), and was positively correlated with easting ($r = 0.75$) and heat load index ($r = 0.70$; Fig. 2a). Variables related to urbanization were positively correlated with Axis 1: development ($r = 0.62$), impervious surfaces ($r = 0.67$), and vehicles ($r = 0.48$). Development was somewhat correlated with easting ($r = 0.33$), since the west side of the basin has the lowest level of development. Axis 2 was negatively correlated with slope ($r = -0.60$) and elevation ($r = -0.41$), and positively correlated with aspect ($r = 0.56$). These patterns primarily reflect the strong precipitation gradient from west to east, with the west sites having high precipitation, high wetness, and late snow-melt date (due to the generally east-facing aspect and shading by dense fir forests), and the east sites having low precipitation and high heat load index (due to the generally west-facing aspect and open Jeffrey pine forests).

Given that environmental conditions were the strongest influence on plant community structure, it is not surprising that the CCA with anthropogenic effects as covariates (E|H) had similar results to those of the CCA with both sets of variables included; the ordination isolating environmental effects (E|H) explained 12.4% of the variation in plant species composition and cover ($p = 0.002$; Table 1b) and had similar variable associations as the analysis with all variables combined. Axis 1 was negatively correlated with wetness ($r = -0.76$) and no-snow date ($r = -0.76$), and positively correlated with easting ($r = 0.71$); axis 2 was negatively correlated with slope ($r = -0.91$).

The ordination isolating anthropogenic effects (H|E) only explained 5.5% of the variation, but showed that impervious surfaces, development, and human activity all influenced plant community composition (Fig. 2b). In H|E, Axis 1 was positively correlated with impervious surfaces ($r = 0.73$), and Axis 2 was negatively correlated with development ($r = -0.72$)

Table 1
Summary of axes for three canonical correspondence analyses to evaluate the combined and individual effects of environmental conditions (E) and anthropogenic effects (H) on plant community composition and structure

	Axis				Total
	1	2	3	4	
(a) H∪E					
Eigenvalues	0.435	0.210	0.117	0.111	
Cumulative percentage variance explained of species data	8.0	11.9	14.1	16.1	
Sum of all canonical eigenvalues					1.209
Total inertia					5.411
Monte-Carlo test *P*-value, all axes	0.002				0.002
(b) E|H					
Eigenvalues	0.274	0.165	0.103	0.073	
Cumulative percentage variance explained of species data	5.5	8.8	10.9	12.4	
Sum of all canonical eigenvalues					0.75
Monte-Carlo test *P*-value, all axes	0.002				0.002
(c) H|E					
Eigenvalues	0.105	0.074	0.038	0.030	
Cumulative percentage variance explained of species data	2.3	4.0	4.9	5.5	
Sum of all canonical eigenvalues					0.26
Monte-Carlo test *P*-value, all axes	0.082				0.084

(a) Combined effects; (b) anthropogenic effects treated as covariates E|H; (c) environmental effects treated as covariates H|E.

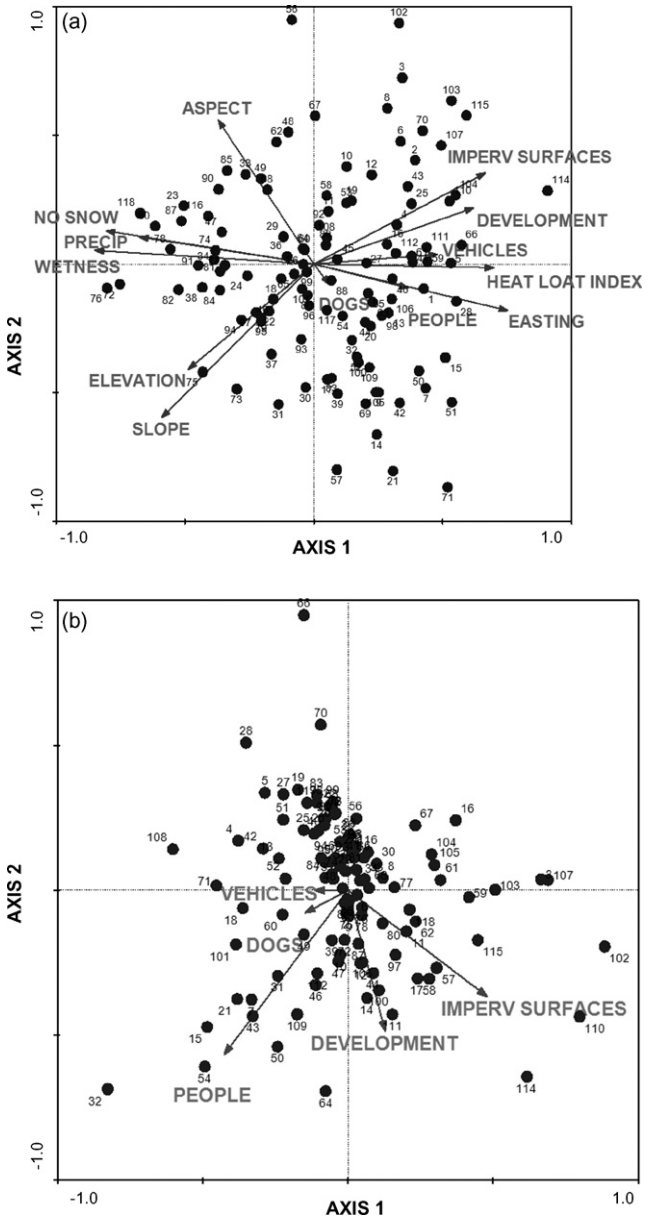

Fig. 2. Canonical correspondence analysis of plant species composition and cover based on (A) all variables and (B) anthropogenic effects with environmental variables as covariates for 118 forested study sites in the Lake Tahoe basin (2003–2004). Biplots display the location of eight environmental variables (snow-melt date [no snow], annual precipitation [precip], soil moisture [wetness], elevation, slope, aspect, heat load index, easting) and five anthropogenic variables (number of unrestrained dogs per hour [dogs], number of people per hour [people], number of vehicles per hour [vehicles], development within 300 m, and impervious surfaces within 300 m [imperv surfaces]).

and people per hour ($r = -0.66$). Neither axis individually was significant, but together they were nearly significant ($p = 0.084$; Table 1c).

Variance partitioning based on the CCA showed that most of the variance was unexplained (77%); however, a substantial portion of the explained 23% of the variation was attributable to anthropogenic variables alone (H|E; 5%) or intersected with environmental variables (H∩E; 4%). In total, 9% of the variation explained by environmental factors examined was attributable to human-influenced conditions.

3.2. Changes in remnant forest stands in response to surrounding development

3.2.1. Plant species richness and cover

Native species richness in remnant forests was not strongly affected by development, based on regression analyses (Table 2). Total species richness increased slightly, but not significantly, with development ($p = 0.082$). Richness and cover trended similarly by life form, indicating no major shift in community dominance. Tree species richness was negatively associated with development, but not significantly ($p = 0.070$). Frequencies of red fir (*Abies magnifica* Andr. Murray) and sugar pine (*Pinus lambertiana* Douglas) were reduced 39.3% and 29.6%, respectively, from lowest to highest development, followed by white fir and incense cedar (*Calocedrus decurrens* [Torrey] Florin; 15.1 and 14.6% reductions, respectively). Canopy closure was not affected consistently by development ($p = 0.376$); however, the cover of trees in the understory was negatively affected by development ($p = 0.002$), suggesting that the density of seedlings and saplings declined with development.

Herbaceous plant species generally increased with development (Table 2). Herb species richness significantly increased with development by 1.9 species (from 10.1 at low-development sites to 12.0 species at high-development sites; $p = 0.050$). Grasses also significantly increased in richness with development ($p < 0.001$), doubling from 1.8 to 4.0 species. Concomitantly, grass and herb cover combined significantly increased in association with development ($p = 0.017$). Shrub species richness was not associated with development ($p = 0.498$), nor was shrub cover ($p = 0.521$). Community dominance also did not appear to be affected by surrounding development for herbs, trees, or shrubs ($p = 0.126$, 0.529, and 0.653, respectively).

Exotic species richness increased significantly with development ($p < 0.001$), although many sample sites in areas with higher development did not have exotic species (Table 2, Fig. 3a). Thirty-six percent of sample sites had exotic species; sites with ≤40% development had <1 exotic plant species on average (mean = 0.4 spp., S.D. = 0.93, range = 0–6), whereas sites with >40% development had nearly 4 exotic plant species (mean = 3.7 spp., S.D. = 3.97, range = 0–15). Exotic species with the greatest frequency of occurrence across the 118 sites were cheat grass (*Bromus tectorum* L.; $n = 18$), orchard grass (*Dactylis glomerata* L.; $n = 17$), dandelion (*Taraxacum officinale* Wigg.; $n = 15$), tall wheat-grass (*Elytrigia pontica* [Podp.] Holub; $n = 11$), common knotweed (*Polygonum arenastrum* Boreau; $n = 8$), and salsify (*Tragopogon dubius* Scop.; $n = 7$).

3.2.2. Forest structure

Few changes in forest structure were indicated by regression analyses (Table 2). Tree density did not change with increases in surrounding development regardless of tree diameter (all, $p = 0.763$; large, $p = 0.326$; medium, $p = 0.247$; small, $p = 0.452$); however, the density of cut stumps did increase with development ($p < 0.001$), and all sites above 60%

Table 2
Analysis of vegetation conditions in remnant forests and surrounding landscape conditions relative to development within 300 m and relative to each other based on linear regression analysis

	Remnant forest vs. development			Landscape vs. development			Remnant forest vs. landscape		
	Dependent variable								
	Slope (*b*)	S.E. (*b*)	*P*-value	Slope (*b*)	S.E. (*b*)	*P*-value	Slope (*b*)	S.E. (*b*)	*P*-value
Remnant forest and surrounding landscape									
Ground cover									
Percent herb cover	0.087	0.036	0.017	<0.001	0.003	0.921	0.016	0.006	0.006
Percent shrub cover	−0.042	0.066	−0.448	−0.448	0.063	<0.001	0.359	0.111	0.001
Percent tree cover	−0.176	0.055	0.002	−0.010	0.002	<0.001	0.009	0.004	0.025
Total log density	−0.043	0.008	<0.001						
Small diameter log density	−0.025	0.005	0.465						
Trees									
All trees	0.101	0.342	0.763	−0.022	0.003	<0.001	0.021	0.005	<0.001
Small diameter trees	−0.657	0.871	0.452	−0.012	0.003	<0.001	0.01	0.006	0.084
Medium diameter trees	0.415	0.356	0.247	−0.020	0.002	<0.001	0.020	0.005	<0.001
Large diameter trees	−0.057	0.058	0.326	0.004	0.002	0.129	−0.005	0.004	0.350
Canopy closure	0.019	0.022	0.376	−0.323	0.056	<0.001	0.473	0.108	<0.001
Dead wood									
Total snag density	0.038	0.006	<0.001	−0.059	0.005	<0.001	0.027	0.009	0.005
Small diameter snag density	−0.020	0.007	<0.001	−0.042	0.005	<0.001	0.03	0.009	<0.001
Large diameter snag density	−0.485	0.005	<0.001	−0.051	0.004	<0.001	0.007	0.008	0.411
Large diameter log density	−0.041	0.008	<0.001	−0.061	0.006	<0.001	0.027	0.011	0.015
Remnant forests only									
Richness									
Native plant species richness	0.010	0.006	0.085						
Tree species richness	−0.011	0.006	0.070						
Shrub species richness	0.009	0.013	0.498						
Herb species richness	0.098	0.049	0.050						
Grass species richness	0.046	0.009	<0.001						
Exotic plant species richness	0.021	0.003	<0.001						
Ground cover									
Herb dominance	0.002	0.001	0.126						
Shrub dominance	0.005	0.001	0.653						
Tree dominance	−0.004	0.001	0.529						
Vertical structure									
Veg. freq. 0–5 m	−0.150	0.004	<0.001						
Veg. freq. 5–10 m	0.043	0.058	0.492						
Veg. freq. 10–15 m	0.028	0.021	0.175						
Veg. freq. 15–20 m	0.036	0.020	0.073						
Veg. freq. >20 m	0.027	0.017	0.114						
No. ht. classes w/veg.	0.006	0.004	0.156						
Woody plants									
Average snag decay class	−0.008	0.002	0.002						
Decadence features	<0.001	<0.001	0.325						
Stump density	0.034	0.006	<0.001						

For regressions involving surrounding landscape sites, percent development was treated as a covariate and site clusters were treated as a random effect, thereby accounting for potential spatial autocorrelation within landscape and remnant forest site clusters.

development had cut stumps. Similarly, the vertical structure of the forest changed with development. The frequency of occurrence of vegetation in the understory (0–5 m) declined significantly with increasing development ($p < 0.001$), and then appeared to increase slightly but not significantly with development in each of the height classes above 10 m (10–15 m, $p = 0.175$; 15–20 m, $p = 0.073$; >20 m, $p = 0.114$). Overall, the number of height classes with vegetation increased slightly, but not significantly, with development ($p = 0.156$).

Dead woody material, by multiple measures, was significantly reduced in association with development (Table 2, Fig. 3b, c). The main pattern of the decline in both snags and logs was a reduction in maximum values observed as development increased. Snag density declined significantly with increasing development, including total snag density and both diameter classes (all snags, $p < 0.001$; small, $p < 0.001$; large, $p < 0.001$). A large drop in the range of snag densities was observed at elevated levels of development (>10%): moderate- (10–40%) and high-development (>40%) sites

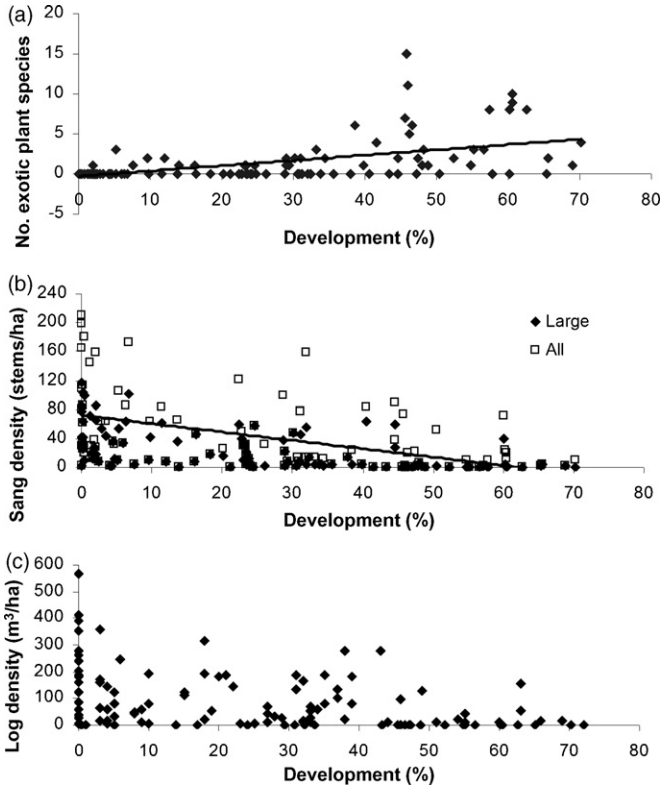

Fig. 3. Simple linear regression of (a) exotic plant species richness, (b) snag density (stems/ha; large snags ≥31 cm dbh), and (c) log density (m^3/ha) by land development within 300 m. Data were collected at 118 sites in the Lake Tahoe basin, 2003–2004.

combined showed an 80% reduction in the proportion of sites with ≥50 snags per ha compared to low-development sites (9% vs. 40%, respectively). Log density also declined significantly with increasing development ($p < 0.001$), reflecting reductions in large-diameter logs ($p < 0.001$) as opposed to small-diameter logs ($p = 0.465$). As with snags, log density dropped substantially with increases in development, showing two thresholds of change at 10% and 40% development. Moderate- and high-development sites showed an 86% reduction in the proportion of sites with >200 m^3/ha of logs compared to low-development sites; (4% vs. 29%, respectively). Only one of the 30 high-development sites exceeded >200 m^3/ha of logs (<1% of sites).

The condition of snags and logs also changed with development (Table 2). There was a significant decline in the average decay class of snags ($p = 0.002$, $n = 105$ sites with snags), representing primarily a loss of soft (decay class 4 or 5) snags ($p < 0.001$). There was a non-significant yet consistent decline in the average decay class of logs ($p = 0.117$, $n = 95$ sites with logs). Development had no relationship with presence of one or more decadence features ($p = 0.325$), so it appears that the lack of snags and logs in more developed areas was most likely the result of removal by people as opposed to reduced mortality rates.

3.3. Changes in the surrounding landscape in response to development

Simple linear regressions showed that, in contrast to remnant forests, almost all measures of forest structure changed with development in the surrounding landscape (Table 2). Density of small- and medium-diameter trees declined significantly with development ($p = 0.001$ and $p < 0.001$, respectively); however, large-tree density did not change with development ($p = 0.129$). Total tree density mirrored the decline in small- and medium-diameter trees ($p < 0.001$). Total snag density similarly declined significantly with development ($p < 0.001$). Small- and large-diameter snags both declined significantly ($p < 0.001$ for both). Log density also declined significantly with development ($p < 0.001$).

Herbaceous plant cover did not vary substantially with development in the surrounding landscape ($p = 0.921$). However, woody plant cover did decline, with shrub cover and tree canopy closure declining significantly with development ($p < 0.001$ for both), in contrast to remnant forests.

3.4. Remnant forest compared to the surrounding landscape

Bar graphs of remnant-forest and surrounding-landscape conditions indicated strong trends within and among site types (Fig. 4), and statistical comparisons (using ANCOVA) showed that many elements of forest structure differed between these two types of sites even when the influence of development was removed (Table 2). Tree density did not decline in remnant forests as opposed to the surrounding landscape ($p < 0.001$), driven by differences in the higher density of medium-diameter trees ($p < 0.001$) and, to a lesser degree, small-diameter trees ($p < 0.084$) in remnant forests. Medium- and small-diameter trees had similar densities in remnant forests and in the surrounding landscape at low development, but density steadily declined in the surrounding landscape with increasing development (Fig. 4a). Large-diameter trees, alternatively, did not differ significantly in their density between the two site types ($p = 0.350$). Snag densities declined with development to a greater degree in the surrounding landscape compared to remnant forests ($p = 0.005$), due largely to greater losses of small snags ($p < 0.001$) as opposed to large snags ($p = 0.411$). Snag density was similar in remnant forests and the surrounding landscape where development was low, and snag density declined by over half at both types of sites in moderate–high development, but the surrounding landscape continued to decline in snag density such that high-development sites rarely contained snags (Fig. 4b).

Log density declined more dramatically in the surrounding landscape compared to remnant forests ($p = 0.015$), following the same trend observed for snag densities between the two types of sites (Table 2). Log density was 23% higher in remnant forests than in the low-development surrounding landscape, but the discrepancy widened considerably at higher development levels (Fig. 4b). At moderate development levels, remnant forest sites had twice the log densities of surrounding-landscape sites (85 and 42 m^3/ha, respectively). At high development levels, remnant forest sites still retained an average of 61 m^3/ha

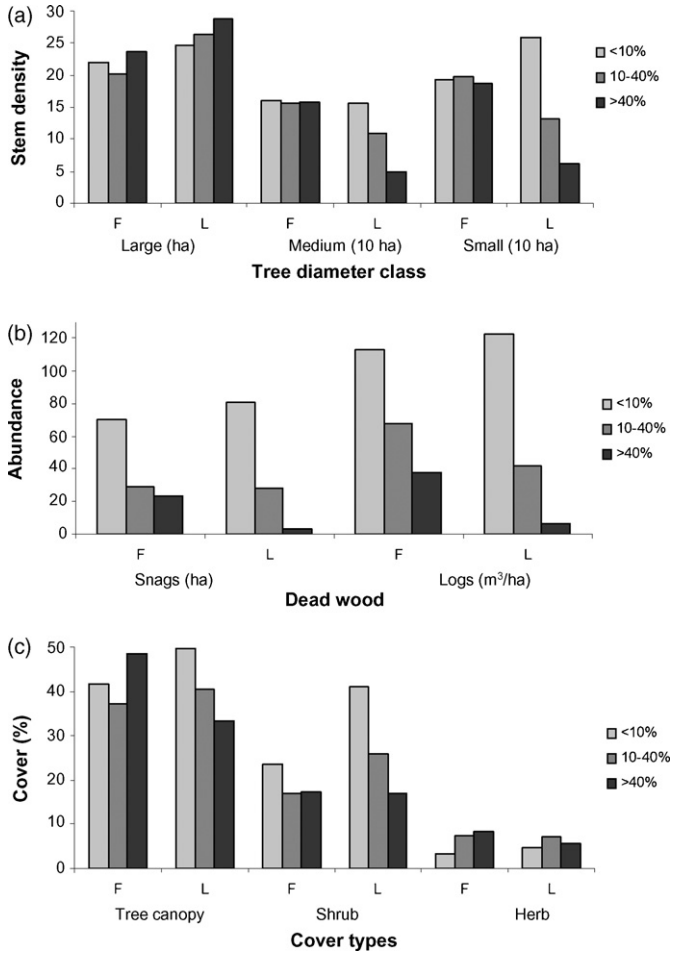

Fig. 4. Comparative changes in average values for three metrics of forest structure along a land development gradient in remnant forest stands (F) and the surrounding landscape (L) based on average values for three measures of forest structure (a, tree diameter class; b, dead wood; c, cover type) across three levels of land development within 300 m (<10%, 10–40%, >40%). Data were collected at 75 sample sites in the Lake Tahoe basin, 2003–2004.

of logs, whereas they were nearly absent from surrounding-landscape sites (Fig. 4b).

Most measures of vegetation closure and cover also differed between the two types of sites (Table 2). Canopy closure declined in the surrounding landscape, whereas it did not do so in remnant forests ($p < 0.001$); however, canopy closure for all sites and conditions was close to or exceeded 40% except when development exceeded 40%. Shrub cover was significantly lower in remnant forests than in the surrounding landscape ($p = 0.001$), but this difference was a function of a greater prevalence of shrub-dominated vegetation in the surrounding landscape (nearly twice as high on average; Fig. 4c), reflecting the fact that we selected forested conditions to represent remnant sites. Shrub cover declined with development in the surrounding landscape such that moderate- and high-development sites were similar in cover to forested sites (Fig. 4c). Herbaceous plant cover increased in remnant forests with development, whereas it remained relatively constant in the surrounding landscape ($p = 0.006$; Fig. 4c).

4. Discussion

Maintaining the integrity of remnant forests requires careful attention to composition, structure, and function, and in many cases may require human intervention to compensate for unavoidable degradations in ecosystem services. We observed that urban land development and human activity were correlated with a substantial portion of the variation in plant community composition and structure, as evidenced by the strong association of human factors with the first axis in the CCA and by the association of human factors with nearly one-quarter of the variation explained. Retention of native vegetation is frequently used to maintain ecosystem functions and biological diversity. As other studies have shown, however, as the surrounding landscape experiences land development, the integrity of remnant native vegetation is challenged by a variety of intrinsic and extrinsic factors (e.g., McKinney, 2002, 2006; Hansen et al., 2005).

Native species richness and cover did not decline in remnant forests with increasing urbanization surrounding them, contrary to many previous urbanization studies (Bagnall, 1979; Airola and Buchholz, 1984; Hobbs, 1988; Rudnicky and McDonnell, 1989; Kowarik, 1995; Hill et al., 2002; McKinney, 2002). As a group, only tree species declined in richness with development. Surprisingly, rare native species as a group did not decline with increases in surrounding development, suggesting that extinction rates were low and/or immigration rates were high. As urban land development progresses in landscapes, plant species richness in remnant undeveloped areas typically declines as a function of declining area of remnant patches (smaller areas having higher extinction rates) and increasing habitat loss and fragmentation of the surrounding landscape (causing lower immigration rates; e.g., Jacquemyn et al., 2001; Honnay et al., 2002; Pearson and Dawson, 2005). In our study area, it is likely that local regulations on the extent of site alteration, plus the retention of high connectivity in the surrounding landscape, contributed to maintaining native species richness and the ecosystem functions species perform (Walker et al., 1999; Lyons et al., 2005) in remnant forest stands.

Urban areas appeared to be more susceptible to invasion by exotic species, consistent with other studies of exotics in managed or urbanizing ecosystems (e.g., Godefroid and Koedam, 2003; Schwartz et al., 2006; Seabloom et al., 2006; Collins et al., 2007). Richness and cover of herbs and grasses were also greater in more developed areas, consistent with other researchers' observations that conditions favorable to plant species richness apply to native and exotic species alike (e.g., Stohlgren et al., 1999; Keeley et al., 2003; Stohlgren et al., 2003; Seabloom et al., 2006). Exotic species are recognized as a significant conservation concern, as they have been shown to replace native species and can alter ecosystem functions, such as hydrologic conditions (Vitousek, 1986; Schultz and Mooney, 1994; Lyons and Schwartz, 2001). The low total cover of exotic species and the lack of significantly altered richness, cover, or dominance of native species suggests that there is currently no measurable impact of exotic species on native plant species richness in remnant forests in our study area even at higher

levels of surrounding development. The structure of remnant forests, including high ground cover by native plants, high canopy closure, and low ground disturbance, may result in low invasibility (e.g., Mandryk and Wein, 2006). Although exotic species loads were low in remnant forests, the large number of exotic species suggests that they may pose a risk, if unchecked, to the diversity of native plant species and associated ecosystem functions, such as nutrient cycling (Lyons and Schwartz, 2001), in these forests as disturbance increases with growing urban land development. Invasions of exotic species in urban areas have been attributed to a variety of factors, including ground disturbance, human conveyance, reductions in ground cover of native vegetation through trampling, increased input of nutrients such as nitrogen and phosphorus, and greater water availability (e.g., Hobbs and Huenneke, 1992).

Development had the most significant effects on forest structure. The dominant forest structure was not highly altered in remnant forests; total tree density within remnant forests did not decline significantly with increasing surrounding development, similar to the findings of Blewett and Marzluff (2005) in the Seattle area, but contrary to the findings of studies in other urbanizing landscapes (e.g., Rudnicky and McDonnell, 1989). Understory tree density and the associated canopy cover of trees, however, did decline with development in remnant forests and the surrounding landscape, as did total tree density in the surrounding developed landscape (primarily as a function of reduced small- and medium-diameter tree density). These changes have significant ecological implications, namely altered recruitment, microclimatic conditions, vertical diversity, and a more open understory, creating a park-like structure. Interestingly, these changes may be moving forest structure closer to historical conditions, based on reconstructions (Taylor, 2004) and measurements from similar unmanaged forests (Stephens, 2004; Stephens and Gill, 2005) that suggest that historical Jeffrey pine and white fir forests had lower small-tree densities.

The reduction in the number and condition of snags and logs appeared to be a function of removal through vegetation management, as opposed to a change in tree mortality, since tree disease symptoms and decadence features were not more common in highly urbanized areas; light foliar color, oozing sap, and leaf necroses were common for all conifer species at our sample sites, regardless of proximity to development. Reductions in snags and logs with development, particularly those in more advanced stages of decay, are consistent with other studies of remnant forests in urban areas (e.g., Blewett and Marzluff, 2005; Fraterrigo and Wiens, 2005). Although reductions in snags and logs occurred across the development gradient, regardless of the location of the site, they were more pronounced in the surrounding landscape compared to remnant forests, indicating that remnant forests retained a greater degree of ecological integrity. It is likely, however, that current densities of snags and logs in unmanaged forests are extreme, resulting from clear-cutting early in the 20th century followed by a century of fire suppression and limited timber harvest. The historical fire regime of frequent, low- to moderate-severity fires was likely to have regulated the accumulation of dead wood (Skinner, 2002).

Standing and down dead wood serve many important ecosystem functions in forests. For example, decomposing logs play a role in nutrient and carbon cycling (Brunner and Kimmins, 2003; Zielonka and Piatek, 2004) and in the maintenance of soil structure through long-term inputs of humus. Snags and logs also provide essential habitat (e.g., nest sites, cover, foraging substrates) for many species of vertebrates and invertebrates (e.g., Bull et al., 1997; Bull, 2002; Lindgren and MacIssac, 2002; Machmer, 2002; Maguire, 2002), and host numerous bacteria and fungi (Zielonka and Piatek, 2004). Hunter (2005) suggests that snags and logs are candidate mesofilters for conservation, meaning that they represent an important bridge between coarse-filter strategies, which define areas set aside to meet conservation objectives, and fine-filter strategies, which focus on the needs of individual species. Mesofilter strategies focus on features that are critical to the welfare of many species and processes. The mesofilter concept applies well to the management of remnant forests and places appropriate importance on the conservation of snags and logs in managed landscapes.

Many social factors affect the management of vegetation in proximity to built environments. In the basin, as in many urban–wildland interface areas, reducing the threat of fire is a high priority (Stephens and Ruth, 2005). The Sierra Nevada in general has been subject to fire suppression for over a century, resulting in ecological and human safety problems, such as altered forest structure, increased tree density, increased accumulation of dead wood, increased insect outbreaks, lowered biodiversity, and vulnerability to catastrophic fires (McKelvey and Johnson, 1992; Elliot-Fisk et al., 1996; Ferrell, 1996; McKelvey et al., 1996; Keeley et al., 2003). The Lake Tahoe basin is no exception, with a large proportion of forests in the lower montane zone having been subject to intensive logging to supply wood to Nevada silver mines, followed by 100 years of fire suppression (Elliot-Fisk et al., 1996; Ferrell, 1996; Lindström, 2000; Maloney and Rizzo, 2002). In attempts to reduce the threat of high impact wildfire, such as the recent 1200 ha Angora wildfire that destroyed over 200 homes in the Lake Tahoe basin (O'Toole, 2007), management agencies make fuel reduction a top priority.

Fuel reduction activities can include overstory and understory thinning, creation of forest openings, and prescribed burning, all of which reduce the amount of woody material (live and dead) from a site (e.g., Tahoe Regional Planning Agency, 2004; Agee and Skinner, 2005; Passovoy and Fule, 2006; Collins et al., 2007); however, treatment outcomes vary depending on the methods used (Stephens and Moghaddas, 2005). Snags, and to a lesser extent logs, also pose an increased threat of fire (Agee and Skinner, 2005), so they are frequently reduced or removed as part of fire management activities, even in less developed areas.

In addition, passive management activities by local residents can contribute to the loss of standing and down woody material (e.g., Matlack, 1993), as well as changes in vegetation. Snags are commonly removed in areas with high recreation use or

near houses and roads because of concerns that they may fall. Logs and snags are often the target of firewood gathering activities as well. Remnant native vegetation is sometimes manicured to be more pleasing to the eye or easier for people to navigate through by reducing the density of the overstory and removing dead woody material (e.g., Tyrväinen et al., 2003).

5. Management implications

Existing conditions of urban forests have resulted from a collage of interdependent social and ecological processes (Walker et al., 2004), few of which have been directed at achieving a desired forest condition. Past forest management was driven by the desire for resource extraction and fire safety. Current forest management is driven by public safety, recreation uses, and local population demands for resources. Current landscape conditions are driven by property values, transportation systems, and the economy, with climate change posing an unknown direction and magnitude of influence in the future. It is becoming increasingly recognized that developed areas have a crucial role to play in the maintenance of native communities (Chape et al., 2005; Pyke, 2007), and the ability to maintain the ecological integrity of native communities in these complex social–ecological systems (see Colfer, 2005) will depend as much on passive management activities invoked by the local population as on active management conducted by accountable agencies. A clear notion of desired conditions for urban forests is an important first step. Given that few true reference conditions exist in the Lake Tahoe basin (Barbour et al., 2002), the compositional, structural, spatial, and temporal parameters of desired conditions will depend on a blend of historical reconstructions (e.g., Taylor, 2004), current ecological capacity, forest dynamics in the context of current and future ''drivers'' of change (Nelson et al., 2006), and societal priorities. The condition of remnant forests in a developed matrix is relatively close to that of more remote forests, and even the developed landscape has retained many elements of native vegetation communities. Thus, the potential is great to conserve or restore the integrity of remnant forests and the forested landscape in the Lake Tahoe basin.

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Appendix A

Vegetation, environmental, and urban development variables derived for each of 118 sample sites in the Lake Tahoe basin. Transformations applied for Canonical Correspondence Analysis CCA) and regression are indicated in parentheses.

Variable	Measure	Transformation
Vegetation		
Species richness	All native, trees, shrubs, herbs, grasses, exotics	sqrt (all native only)
Canopy cover	Mean percent	
Herbaceous cover	Mean percent	
Shrub cover	Mean percent	
Tree density	Trees/ha (all, 12.5–28 cm; >28–61 cm; >61 cm)	
Tree basal area	m^2/ha	
Vertical diversity	Number of height intervals with vegetation, frequency of occurrence of vegetation per height interval (5 m increments to 20 m)	ln(0–5 m only)
Snag density	Snags/ha (all, 12.5–30.5 cm, >30.5 cm)	sqrt (CCA) ln(regression)
Snag volume	m^3/ha	
Snag decay class	Percent in each decay class (range = 1–9; Thomas et al. (1979))	
Log density	m^3/ha (all, ≤28 cm, >28 cm)	
Log decay class	Percent in each decay class (range = 1–5; Maser et al. (1979))	
Stump density	Stumps/ha	ln
Decadence incident	Proportion of trees with one or more types	
Plant species richness	Number of species	sqrt
Exotic plant species richness	Number of species	ln
Plant abundance	Mean percent cover	sqrt
Environmental		
Easting	UTM zone 10, NAD 27	
Elevation	Meters above sea level (a.s.l.)	
Heat load index (HLI)	GIS modeled McCune and Keon (2002)	
Precipitation	Mean annual cm/year from PRISM data, Daly et al. (2002)	
Aspect	Range from 0 to 2 Beers et al. (1966)	
Date of final snow-melt	Julian date as per Barbour et al. (1998)	
Wetness	GIS modeled Crist and Cicone (1984)	
Slope	Percent	
Anthropogenic		
Land development	Percent within 300 m Manley et al. (2006)	
Impervious surfaces	Percent within 300 m Dobrowski et al. (2005)	
Use by dogs	Mean number of unrestrained dogs/h	
Use by people	Mean number of people/h	
Use by vehicles	Mean number of vehicles/h	

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