

Effects of Urban Development on Ant Communities: Implications for Ecosystem Services and Management

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Abstract: Research that connects the effects of urbanization on biodiversity and ecosystem services is lacking. Ants perform multifarious ecological functions that stabilize ecosystems and contribute to a number of ecosystem services. We studied responses of ant communities to urbanization in the Lake Tahoe basin by sampling sites along a gradient of urban land development. We sampled ant communities, measured vegetation characteristics, quantified human activities, and evaluated ant-community responses by grouping ants into service-providing units (SPUs), defined as a group of organisms and their populations that perform specific ecosystem services, to provide an understanding of urbanization impacts on biodiversity and their delivery of ecosystem services. Species richness and abundance peaked at intermediate levels of urban development, as did the richness of 3 types of ant SPUs (aerators, decomposers, and compilers). With increasing land development aerator and decomposer ants significantly declined in abundance, whereas compiler ants significantly increased in abundance. Competing models demonstrated that precipitation was frequently among the strongest influences on ant community structure; however, urban development and human activities also had a strong, negative influence on ants, appearing in most models with $\Delta AIC_c < 2$ for species richness and abundance patterns of SPUs and generalists. Response diversity was observed within SPUs, which suggests that the corresponding ecosystem services were maintained until development reached 30–40%. Our data provide evidence that ecosystem functions, such as water infiltration and soil productivity, may be diminished at sites subject to greater levels of urbanization and that conserving ant communities and the ecosystem services they provide could be an important target in land-use planning and conservation efforts.

Keywords: ants, ecosystem services, forest management, Lake Tahoe, service-providing units, water infiltration, urbanization

Efectos del Desarrollo Urbano sobre Comunidades de Hormigas: Implicaciones para los Servicios y Manejo del Ecosistema

Resumen: La investigación que relaciona los efectos de la urbanización sobre la biodiversidad con los servicios del ecosistema es escasa. Las hormigas realizan múltiples funciones ecológicas que estabilizan los ecosistemas y contribuyen a un número de servicios del ecosistema. Estudiamos las respuestas de comunidades de hormigas a la urbanización en la cuenca del Lago Tahoe mediante muestreos a lo largo de un gradiente de desarrollo urbano. Muestreamos comunidades de hormigas, medimos características de la vegetación, cuantificamos actividades humanas y evaluamos las respuestas de la comunidad de hormigas agrupándolas en unidades proveedoras de servicio (UPS), definidas como un grupo de organismos y sus poblaciones que realizan servicios específicos, para entender los impactos de la urbanización sobre la biodiversidad y sus servicios al ecosistema. La riqueza y abundancia de especies fue mayor en niveles intermedios de desarrollo urbano, igual que la riqueza de tres tipos de UPS (aeradoras, descomponedoras y compiladoras). Con el incremento del desarrollo urbano la abundancia de las hormigas aeradoras y descomponedoras declinó significativamente, mientras que la abundancia de las compiladoras aumentó significativamente. Los modelos opuestos demostraron que la precipitación frecuentemente estaba entre las influencias más

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fuertes sobre la estructura de la comunidad de hormigas; sin embargo, el desarrollo urbano y las actividades humanas también tuvieron una fuerte influencia negativa sobre las hormigas, apareciendo en la mayoría de los modelos con $\Delta AIC_c < 2$ para patrones de riqueza y abundancia de UPS y generalistas. La diversidad de respuestas se observó dentro de las UPS, lo cual sugiere que los servicios del ecosistema correspondientes se mantuvieron hasta que el desarrollo alcanzó 30–40%. Nuestros datos proporcionan evidencia de que los servicios del ecosistema, como la infiltración de agua y la productividad del suelo, pueden disminuir en sitios sujetos a mayores niveles de urbanización y que la conservación de las comunidades de hormigas y los servicios que proporcionan pudiera ser una meta importante de la planificación del uso de suelo y de los esfuerzos de conservación.

Palabras Clave: hormigas, infiltración de agua, Lago tahoe, manejo de bosques, servicios del ecosistema, unidades proveedoras de servicio, urbanización

Introduction

The transformation of natural landscapes to urbanized landscapes is a principal force behind the erosion of biological diversity worldwide (Vitousek et al. 1997; Czech et al. 2000; McKinney 2002); however, few explicit connections have been identified between the effects of urbanization on biodiversity and corresponding effects on the ecosystem services biodiversity provides. Ecosystem services—such as water purification, soil production, carbon sequestration, and climate regulation—provided by the biotic and abiotic components of ecosystems are critical for human well being (Daily 1997). These services can be transformed by human activities that alter the diversity of species with particular ecological roles in animal communities (e.g., Elmqvist et al. 2003; Hooper et al. 2005; Dobson et al. 2006).

The term service-providing unit (SPU) refers to a collection of organisms that provide a particular ecosystem service to humanity in a specific spatiotemporal context (Luck et al. 2003). Although the SPU concept originally referred to populations of individual species, the concept can be expanded to apply to populations of multiple species that provide an ecosystem service. The diversity within SPUs contributes to maintaining or restoring ecosystem functions in the face of environmental perturbations through their differential tolerances and sensitivities to environmental change, known as “response diversity” (Elmqvist et al. 2003). Thus, biological diversity within and among SPUs can be critical to maintaining the ecosystem services that those units support and regulate (e.g., Folke et al. 2004; Kremen 2005; Balvanera et al. 2006).

Ants, in particular, perform many important ecosystem functions (Folgarait 1998; Lobry de Bruyn 1999), such as water infiltration and soil modification (Hölldobler & Wilson 1990, 1995; Agosti et al. 2000), which benefit people by providing ecosystem services of clean water and conserving soil. Moreover, ants and the services they provide appear to be especially vulnerable to environmental changes from human-generated disturbances

(Bestelmeyer & Wiens 1996; Bolger et al. 2000; Thompson & McLachlan 2007), and thus their ability to perform ecosystem functions and provide associated services is compromised, which alters ecosystem resiliency (Nuhn & Wright 1979; Bestelmeyer & Wiens 1996). Despite growing recognition of the ecological importance of ants, there is limited scientific understanding of how urbanization and land management affects ant communities and, in turn, the ecosystem services they provide.

We examined how the biological diversity of a forest-dwelling ant community changed across a gradient of land disturbances associated with urban development. We collected data on abundance and species richness in ant communities to determine the responses of 3 SPUs—aerator ants, decomposer ants, and compiler ants—to urbanization. These ant SPUs perform essential functions that maintain forest health and its incumbent services of clean water, clean air, carbon sequestration, and raw material for wood products, all of notable social importance (e.g., Rapport et al. 1998; Kaufmann 2004; Stephens & Ruth 2005).

The aerator SPU builds complex subterranean tunnel networks that provide for soil aeration, water infiltration, and energy redistribution. Water infiltration rates, in particular, can be 3 to 6 times greater in areas with subterranean nests of aerator ants than in areas without them (Denning et al. 1977; Majer et al. 1987; Lobry de Bruyn & Conacher 1994). The decomposer SPU builds tunnel networks in woody debris and facilitates decomposition and nutrient release by allowing bacteria, fungi, and water to penetrate wood (Knight & Heikkinen 1980; Lindgren & MacIsaac 2002). The compiler SPU builds thatch mounds on the ground that serve to increase soil nutrient availability and contribute to patchiness in vegetation (Petal 1992; Dean et al. 1997; Lobry de Bruyn 1999). Soils near compiler ant nests often have higher mineralization rates of nitrogen and organic matter (Petal & Kusinka 1994; Wagner et al. 1997), even years after nest abandonment (Czerwinski et al. 1971; Lobry de Bruyn 1999). We considered other types of ants in the system to be generalists even though they may be resource specialists in other

contexts and may at times take on the role of aerators, decomposers, or compilers.

We evaluated the effects of urbanization on ant communities to inform management decisions that affect the delivery of forest ecosystem services. We did not quantify the services provided by ant communities; rather, we used the concept of SPUs to frame how we looked at the potential effects of urbanization on ant community diversity and ecological redundancy and the potential consequences for associated ecosystem services and ecosystem resilience. We posed 3 questions: What is the spatial scale at which urban development and associated human activities most affect ant communities, and how does it affect them? What is the relative importance of urban development, human activities, and habitat characteristics in shaping ant communities? And how do ant SPUs respond differentially to urban development, and what might those responses mean for the ecosystem services they provide?

Methods

Study System and Design

The Lake Tahoe basin is located in the central Sierra Nevada on the boundary between California and Nevada (U.S.A.; Fig. 1). This montane basin includes Lake Tahoe and its surrounding 82000-ha watershed and is dominated by coniferous forest ranging in elevation from 1900 m to about 3000 m (Manley et al. 2000). We restricted our study area to the lower montane zone (<2200 m) because most (95%) urban development in the basin is in this ecological zone (Tahoe Regional Planning Agency 2001). In Tahoe, the process of urbanization has been gradual and intentionally low impact, with a high interspersion of natural and developed areas and the retention of many native attributes on developed lands. Forest health is a primary societal concern, with management emphasis on reducing the threat of wildfire, maintaining biological diversity, and restoring the clarity of Lake Tahoe.

We used a development index derived from land-use types and transportation features (roads and trails; Manley et al. 2008) to selected sample sites along an urban land-development gradient. First, we characterized development at the scale of 30 × 30 m grid cells on the basis of land-use type identified on county parcel maps (Tahoe Regional Planning Agency 2001) and identified transportation features primarily from U.S. Department of Agriculture Forest Service digital transportation layers (Cahill et al. 2002). We then used the moving-window feature of ArcGIS (ESRI 2002) to assign a “percent developed” value to each grid cell on the basis of the percentage of developed land within a 300-m radius. Grid cells were classified into 1 of 6 development classes on the basis of the percentage of developed land within 300 m of a



Figure 1. Distribution of urban development in Lake Tahoe basin (Nevada and California, U.S.A.) with development values expressed as a percentage of developed land area.

sample point (range of values: no development, >0% to 15%, >15% to 30%, >30% to 45%, >45% to 60%, and > 60%). We randomly selected an equivalent number of sites from each of the 6 development classes for a total of 102 sample sites.

Data Collection

Sites were surveyed over 2 years (2003–2004) in June and July. A diversity of site characteristics (e.g., development, location in the basin) was represented in each survey year to avoid confounding survey year with other environmental influences. We used a standard pitfall-trapping method to quantify ant species richness and abundance because it provides rapid and repeatable results and an

unbiased sample of ants within an area (Anderson 1990; Agosti et al. 2000). At each site we used an array of 12 pitfall traps in a 40 × 40 m grid located at the center of the site. We placed 4 traps 10 m apart along each of 3, 40-m transects separated by 20 m (Bestelmeyer & Wiens 1996; Anderson 1997). Pitfall traps consisted of 6.5-cm diameter (120 mL) plastic cups containing 25 mL of propylene glycol and remained open for 7 days.

We collected field data on forest vegetation structure (for further reference, see Heckmann et al. 2008) and human use (people and domestic animals) at a randomly selected subset of 63 sites to determine their added influence on ant SPUs. We measured a suite of habitat characteristics commonly associated with the occurrence and abundance of ant species. We measured tree density for each of 3 diameter-at-breast-height (dbh) classes in concentric circular plots: all trees >12.5 cm diameter within a 7.3-m radius, trees >28 cm within 56.4-cm radius, and trees >61 cm within a 30.5-m radius. We used 3 line-intercept transects (30 m) to estimate vegetation cover and coarse woody debris. We estimated vegetation cover every third meter along transects for a total of 10 1-m segments. For each segment we estimated the proportion of each meter occupied by all plant species. We also recorded the volume and decay class of coarse woody debris (logs >10 cm diameter) that intersected transects (see Casey et al. 1995), categorized sites as burned or not burned on the basis of visual evidence of past fires within the site, and estimated average annual precipitation for each site on the basis of PRISM data on the 30-year average (1971–2000) (Daly et al. 2002).

To characterize human use, we established 1.2 km of survey routes and 5 count stations within a 200 × 200 m (4 ha) sample unit centered on the pitfall grid. Transect lengths were proportionally reduced in sites of <4 ha. We walked transects at a pace of 33 m/min and stopped at 5 designated points for 3 min. We recorded all encounters with humans and pets, distance to detections, and locations of users. Each site was surveyed once per week, with one survey allocated to each combination of time of day (dawn to midday, midday to evening) and segment of week (weekday not a holiday, weekend, and holiday) over 5 months (May through September).

Ant Community Measures

All ants captured were identified to species. We assigned membership to the 3 SPUs on the basis of published life-history characteristics (Wheeler & Wheeler 1986) and field observations from other studies (P. S. Ward, personal communication). Species that did not have specialized functions were grouped into a generalist SPU to provide a context for observations of true SPUs. We calculated ant species richness per site, mean species richness per trap per site, total abundance across all species per site, and total abundance per site for each species and for all

species combined in each of the 3 SPUs and for generalists. Species richness per site provided a measure of the total species pool at a site. Mean species richness per trap per site provided a measure of microsite diversity, reflecting the conditions to which most ants are confined in their daily activity patterns (generally <10 m from their nest).

We transformed the number of individuals captured into an ordinal 6-point scale of abundance according to standard methods (Anderson 1997): 1, 1 ant; 2, 2–5 ants; 3, 6–10 ants; 4, 11–20 ants; 5, 21–50 ants; 6, ≥50 ants). This scaling transformation minimized distortions caused by large numbers of individuals falling into small numbers of traps due to trap placement near nests or foraging trails. Abundance per species per site was calculated as the sum of abundance scores across the 12 traps. We calculated abundance per SPU as the sum of the site scores across member species. For analysis, abundance values were rescaled to a percentage of their theoretical maximum (e.g., abundance value of 72 for an individual species).

Data Analysis

To compare the spatial effects of urbanization, we used coefficients of determination (i.e., adjusted R^2 values) from univariate regressions of each of the 7 ant-community metrics relative to each of 5 different spatial scales of urban development (area developed within 60 m, 100 m, 300 m, 500 m, and 1000 m). Polynomial regressions were used to determine whether there was a linear or quadratic relationship between independent and response variables. These comparisons allowed us to evaluate the scale at which the ant community responded to development (Tilman & Lehman 2001; Steffan-Dewenter et al. 2002; Kremen et al. 2004) and at which further analyses of urban development should be conducted and to identify variation in responses to development at different spatial scales by SPUs and their constituent species. We plotted the proportional abundance of each SPU against the percentage of development within 60 m to examine changes with land development within and among SPUs. Proportional abundance was calculated for each SPU at each site as the total rank abundance within an SPU divided by the total rank abundance across all SPUs at a site. This proportion was then rescaled from zero to one. We considered relationships with a $p \leq 0.05$ significant.

To compare the relative importance of different environmental factors in shaping ant-community attributes and measures described above, we used multiple regression with Akaike's information theoretic analyses (AIC) for model selection (Burnham & Anderson 2002). A priori, we identified 4 environmental factors (with multiple parameters representing each factor): development, human use, habitat, and precipitation (Table 1). We

Table 1. Explanatory factors and their minimum and maximum values across 102 sample sites in the Lake Tahoe basin that were used in multiple-regression analyses to explain patterns of ant community metrics.

Factor	Variable description	Min	Max
Development	urban development within 60 m of a site (%)	0.00	64.40
	urban development within 1000 m of a site (%)	0.50	63.20
Human use	occurrence of dogs (no./h)	0.00	6.00
	occurrence of humans (no./h)	0.00	428.20
	occurrence of vehicles (no./h)	0.00	215.70
Precipitation	precipitation at site (mm)	493.00	1138.00
Habitat	burned (1) or not burned (0)	0.00	1.00
	volume of coarse woody debris (cm ³ /ha)	0.00	55.90
	tree density (no. per ha)	35.50	1062.20
	total vegetation cover (%)	0.48	1.54

selected development at 60 m as a measure of development at smaller spatial scales, because all ant SPUs responded strongly to urbanization at this spatial scale, and at 1000 m as a measure of development at larger spatial scales. We compared the relative importance of 10 models: each factor individually, all possible pairwise combinations of the factors, and all 4 factors combined (full model). Models were ranked on the basis of their AIC_c values (Δ AIC_c), where the best model has the lowest AIC_c score. Differences in AIC_c scores of <2 indicate substantial evidence for alternative models, differences ≥ 2 indicate that alternative models range from having considerably less support (differences of 2 to 9) to being very unlikely (differences ≥ 10 ; Burnham & Anderson 2002; Johnson & Omland 2004). Akaike weights (w_i) indicate the relative support of one model in comparison with other competing models. We standardized ($y = (y_i - \bar{y})/s$; Quinn & Keough 2002) dependent variables prior to analyses and used PROC REG in SAS 9.1 (2003) for the analysis.

We also assessed differential patterns of response of species within and among SPUs to evaluate response diversity along the urban development gradient (Elmqvist et al. 2003). We used one-way analysis of variance (ANOVA) to evaluate changes in response diversity on the basis of 4 measures (richness, abundance, diversity, and dominance) for each SPU across 3 levels of development within 60 m and 100 m: none (<1%), low (1–30%), and high (>30%) development. We used McIntosh's index (U) to evaluate diversity (Eq. 1) and the Berger–Parker index (d) to evaluate dominance (Eq. 2; Magurran 2003):

$$U = \sqrt{\sum n_i^2} \quad (1)$$

$$d = N_{\max}/N, \quad (2)$$

where n_i is the proportional abundance of the i th species, N is the total number of individuals, and N_{\max} is the number of individuals in the most abundant species.

Pairwise comparisons of development levels were conducted for significant ANOVAs with Bonferonni adjustments. We used histograms of the average rank abundance of individual species per development level to determine the occurrence of compensatory responses among species within SPUs. Only species with average rank abundance of ≥ 1 individual were displayed, with the exception of compiler species, which all had average rank abundances of <1 individual. We considered values significant at $p < 0.1$.

Results

We detected 42 species of ants (31,603 individuals) from 3 subfamilies from our sample sites: 3 dolichoderine species, 12 myrmicines, and 27 formicines. (A list of all species observed is available from M.S.) Aerators were the most species rich and abundant of the SPUs (19 species and 42% of all individual ants). There were only 7 species of decomposers, but they represented 23% of all individuals. Compilers, with just 4 species, comprised only 2.5% of individuals. Six ant species were generalists; these species comprised 32% of individuals. Across all sites, aerator and decomposer groups were made up of multiple species with total rank abundance values of ≥ 200 . All 4 compiler species had relatively low abundance, with total rank abundance values of ≤ 30 (Fig. 2).

Spatial Relationships with Urban Development

Ant species richness per site had the strongest quadratic response to urban development where development occurred within 300 m of sample sites (adj. $R^2 = 0.14$, $p = 0.001$), as did ant species richness per trap ($p = 0.048$). Ant richness per site also responded significantly to development within 500 m (adj. $r^2 = 0.04$, $p = 0.016$) and 1000 m (adj. $r^2 = 0.03$, $p = 0.035$). Both measures of ant species richness demonstrated a quadratic fit to the data where development occurred within 300 m, and species richness was greatest at sites with levels of development between 30–40% (Fig. 3). Total ant abundance

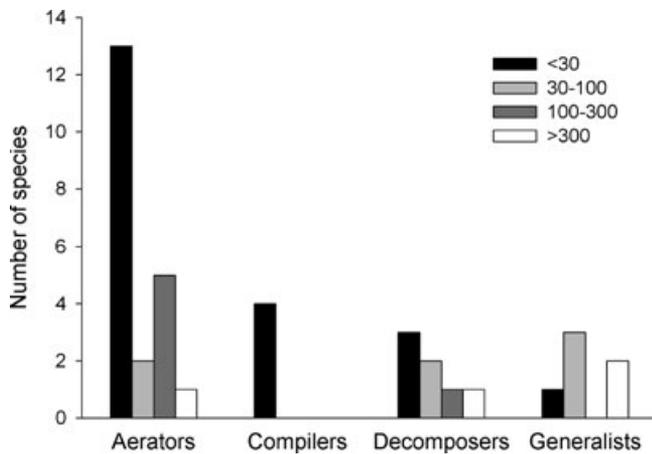


Figure 2. Number of species in each of 4 ant groups (3 service-providing units and generalists) occurring in 4 categories of total rank abundance on the basis of the contents of 12 pit-fall traps at each of 102 sample sites in the Lake Taboe basin, 2003–2004.

demonstrated significant negative responses to urban development at 300 m (adjusted $r^2 = 0.11$, $p = 0.004$), 500 m (adj. $r^2 = 0.13$, $p = 0.001$), and 1000 m (adj. $r^2 = 0.09$, $p = 0.01$) scales. A quadratic regression was the best fit to development at the 300-m scale (adj. $r^2 = 0.14$, $p = 0.001$) and showed a peak at 30–40% development (Fig. 3). None of the community-wide measures were significantly associated with development at 60 m and 100 m.

Abundance patterns of SPUs were generally and significantly associated with urban development only at more localized spatial scales (60–300 m). The abundance of aerators demonstrated a significant quadratic relationship with development at the 60-m scale (adj. $r^2 = 0.08$, $p = 0.018$). Their abundance increased slightly at low levels of development and declined consistently with development (Fig. 4). Significant decreases of decomposers occurred in response to development at 60-m (adj. $r^2 = 0.09$, $p = 0.016$) and 100-m scales (adj. $r^2 = 0.07$, $p = 0.025$), whereas compilers increased significantly with greater development at 60-m (adj. $r^2 = 0.17$, $p < 0.001$), 100-m (adj. $r^2 = 0.13$, $p = 0.002$), and 300-m scales (adj. $r^2 = 0.07$, $p = 0.037$). Decomposers and compilers generally had linear responses to urban development (Fig. 4). The abundance of generalist ant species demonstrated a significant response to development at the 60-m scale (adj. $r^2 = 0.11$, $p = 0.029$); the relationship exhibited a quadratic form with lowest abundance occurring at moderate levels of development (Fig. 4).

Relative Influence of Environmental and Human Factors

Community-wide measures were all strongly influenced by precipitation, development, and human use on the basis of multiple-regression analyses (Table 2). Our comparisons of competing models to explain species richness

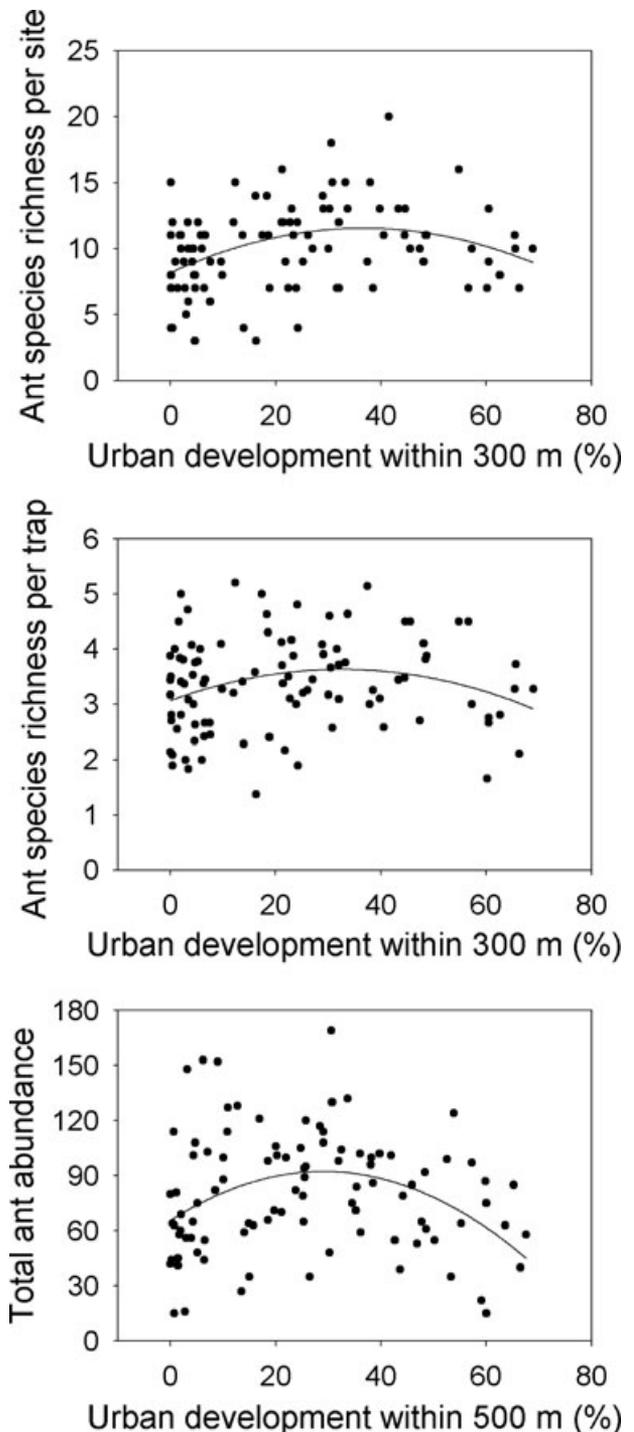


Figure 3. Patterns of ant species richness per site and per trap per site and total abundance relative to the percentage of urban development within 300 and 500 m of a site (quadratic regression models fitted to the data).

per site indicated a strong negative influence of precipitation ($w_i = 0.75$). Models containing the factors habitat, human use, or development had little support, with substantially lower AIC_c scores and weights. Alternatively,

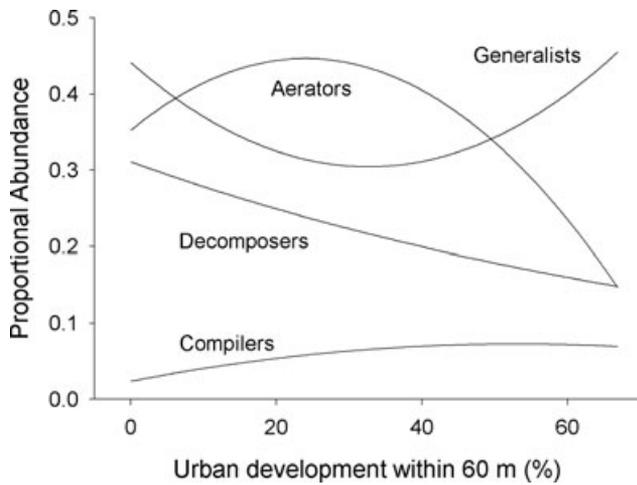


Figure 4. Patterns of ant abundance for 3 service-providing units (aerators, decomposers, compilers) and generalist ants when urban development is within 60 m of a site.

there was strong support for 2 models of ant species richness per trap: the full model ($w_i = 0.38$) and development and human use together ($\Delta AIC_c = 0.10$, $w_i = 0.36$). Comparisons of competing models to explain variation in ant abundance demonstrated a strong positive influence for the precipitation model ($w_i = 0.42$) and negative influence for development ($\Delta AIC_c = 1.81$, $w_i = 0.17$). Habitat was a weak, negative third model ($\Delta AIC_c = 2.14$, $w_i = 0.14$).

Competing models to explain variation in the abundance of SPU and generalists all demonstrated responses associated with urban land development (Table 2). Aerators were most strongly and negatively influenced by the habitat characteristics we measured ($w_i = 0.34$) (tree density, vegetation cover, and coarse woody debris). Aerators were also negatively influenced by human use ($\Delta AIC_c = 1.50$, $w_i = 0.16$) and positively influenced by precipitation ($\Delta AIC_c = 1.68$, $w_i = 0.15$). Decomposers responded most strongly and positively to precipitation ($w_i = 0.49$), but the development + precipitation model ($\Delta AIC_c = 2.02$, $w_i = 0.18$) was also moderately influential. For compilers, the development + human use model ($w_i = 0.74$) was most important, with limited support for other models. Generalist ants were most influenced, and negatively so, by the development model ($w_i = 0.51$) and were positively influenced by the development + precipitation model ($\Delta AIC_c = 1.00$, $w_i = 0.31$).

Response Diversity along the Development Gradient

Species richness, abundance, and dominance of aerator ants all varied significantly among levels of development where it occurred within 100 m of sample sites ($F = 4.24$, $p = 0.017$; $F = 3.03$, $p = 0.053$; and $F = 2.66$, $p = 0.075$, respectively). Aerator species richness and

Table 2. Akaike's information criterion (AIC_c) and Akaike weights (w_i) in a comparison of regression models that describes variance in ant community diversity on the basis of 3 community-wide measures (species richness per site, species richness per trap per site, and total ant abundance) and ant service-providing units.

Models	k	AIC_c	ΔAIC_c	w_i
Species richness per site				
precipitation	1	138.67	0.00	0.75
precipitation + habitat	5	142.89	4.23	0.09
development + precipitation	3	142.98	4.31	0.09
habitat	4	145.11	6.44	0.03
human use	3	146.20	7.53	0.02
development	2	146.55	7.88	0.01
human use + habitat	7	149.00	10.34	0.00
development + habitat	6	149.30	10.64	0.00
development + human use	5	150.71	12.05	0.00
full model	10	152.48	13.81	0.00
Species richness per trap				
full model	10	-17.53	0.00	0.38
development + human use	5	-17.43	0.10	0.36
development	2	-15.50	2.03	0.14
development + precipitation	3	-13.29	4.24	0.05
precipitation	1	-12.64	4.89	0.03
human use	3	-11.95	5.58	0.02
development + habitat	6	-9.79	7.74	0.01
habitat	4	-8.51	9.02	0.00
precipitation + habitat	5	-6.45	11.08	0.00
human use + habitat	7	-5.13	12.40	0.00
Ant abundance				
precipitation	1	430.46	0.00	0.42
development	2	432.27	1.81	0.17
habitat	4	432.59	2.14	0.14
human use	3	433.42	2.97	0.10
development + precipitation	3	434.20	3.75	0.06
precipitation + habitat	5	434.95	4.49	0.04
development + human use	5	435.87	5.41	0.03
development + habitat	6	436.48	6.03	0.02
human use + habitat	7	438.43	7.97	0.01
full model	10	442.82	12.36	0.00
Aerators				
habitat	4	313.73	0.00	0.34
human use	3	315.23	1.50	0.16
precipitation	1	315.41	1.68	0.15
precipitation + habitat	5	315.80	2.07	0.12
human use + habitat	7	316.53	2.80	0.08
development	2	317.51	3.78	0.05
development + human use	5	318.10	4.37	0.04
development + habitat	6	318.50	4.78	0.03
development + precipitation	3	319.45	5.73	0.02
full model	10	319.78	6.06	0.02
Decomposers				
precipitation	1	329.89	0.00	0.49
development + precipitation	3	331.91	2.02	0.18
development	2	332.91	3.02	0.11
precipitation + habitat	5	333.88	4.00	0.07
habitat	4	334.07	4.19	0.06
human use	3	334.21	4.33	0.06
development + habitat	6	336.86	6.98	0.01
development + human use	5	337.22	7.33	0.01
full model	10	338.11	8.22	0.01
human use + habitat	7	338.97	9.08	0.01
Compilers				
development + human use	5	208.13	0.00	0.74

continued

Table 2. (continued)

Models	k	AIC _c	ΔAIC _c	w _i
human use	3	211.45	3.32	0.14
full model	10	213.64	5.50	0.05
development	2	214.50	6.37	0.03
development + precipitation	3	216.09	7.95	0.01
human use + habitat	7	216.26	8.12	0.01
development + habitat	6	216.38	8.25	0.01
habitat	4	218.55	10.42	0.00
precipitation	1	219.31	11.18	0.00
precipitation + habitat	5	220.75	12.62	0.00
Generalist ants				
development	2	375.23	0.00	0.51
development + precipitation	3	376.23	1.00	0.31
precipitation	1	379.00	3.77	0.08
development + habitat	6	380.67	5.43	0.03
development + human use	5	380.96	5.72	0.03
human use	3	381.61	6.38	0.02
habitat	4	383.17	7.94	0.01
precipitation + habitat	5	384.98	9.74	0.00
full model	10	388.30	13.07	0.00
human use + habitat	7	387.45	12.22	0.00

abundance peaked at intermediate levels of development, whereas dominance was highest at sites with no development. We observed a pronounced compensatory shift in dominance between the 2 dominant species within the aerator SPU (Fig. 5a): *Formica* cf. *sibylla* abundance decreased across development levels, whereas *Formica sibylla* abundance increased across development levels.

The abundance and diversity index of decomposer ants changed significantly across levels of development within 60 m ($F = 3.09$, $p = 0.050$; and $F = 2.97$, $p = 0.056$, respectively), dropping at high development. We observed a compensatory shift in abundance among decomposer species with increasing development. *Camponotus modoc* was dominant and, along with *Formica aserva*, reached its highest abundance at low development and then declined at high development. In contrast, *Formica accreta* was lowest in abundance at low development, but became codominant with *C. modoc* at higher levels of development (Fig. 5b).

All 4 measures of diversity for compilers varied significantly among levels of development within 60 m (richness: $F = 4.96$, $p = 0.009$; abundance: $F = 2.96$, $p = 0.057$; dominance: $F = 3.25$, $p = 0.043$; diversity: $F = 2.80$, $p = 0.066$); undeveloped sites were the lowest for all measures. *Formica obscuripes* increased in abundance and became the most dominant species at high development levels over *Formica integroides* and *Formica ravidia*, which were highest in abundance at low development, but declined in abundance at higher levels of development (Fig. 5c).

As expected, generalists appeared to readily adapt to sites altered by development and human use, with no measures of diversity differing significantly among levels of development within 60 m. Similarly, we did not

observe differential patterns of response among species across development levels (Fig. 5d).

Discussion

Our results identified several community changes expressed as shifts in richness and abundance within and among facets of the ant community and demonstrated that both land development around and human use of urban forests can affect ant diversity, even on landscapes that retain substantial components of native vegetation. Land development and disturbance at 30–40% appeared to be the level above which ant diversity began to decline, revealing that ants and the ecosystem services they provide are vulnerable to degradation in response to urbanization.

Ant species richness and abundance both responded unimodally to development at the neighborhood scale (300–500 m), appearing to peak at intermediate levels of land development. These results suggest that ants, despite their confined movements, are affected by environmental alterations in surrounding landscapes. This unimodal response pattern is likely to be a function of a peak in within-patch spatial heterogeneity created by ground disturbance from human activities and forest management, both of which were observed to increase with surrounding urban development. Thus, ant diversity is robust to limited amounts of urban land development and use, but starts declining as human uses begin to dominate the landscape.

We observed compensatory shifts in abundance between the 2 dominant SPUs (aerators and decomposers) and generalists as land development within 60 to 100 m of these ant communities increased. At low levels of development, those 2 SPUs and generalists were similar in abundance, whereas at the highest levels of development, generalists were over twice as abundant as any of the SPUs. This compensatory shift suggests that higher levels of land development resulted in a loss of ecosystem services through reductions in aerators and decomposers. Generalists may perform some of the same ecosystem services, but because of their opportunism, these services are likely to fluctuate with conditions and offer a much-reduced contribution to ecosystem stability and resilience. Dominance of a few generalist species also represents a potential loss of ecosystem resilience because species composition is more homogeneous among sites (Hooper et al. 2005).

Ant SPUs were all influenced by localized urban development to varying degrees, and human land use had a strong influence on the abundance of aerator and compiler ants. It is understandable that these 2 SPUs would be more vulnerable to changes associated with human use within a site, such as soil compaction and ground disturbance, than decomposer ants, which are most likely

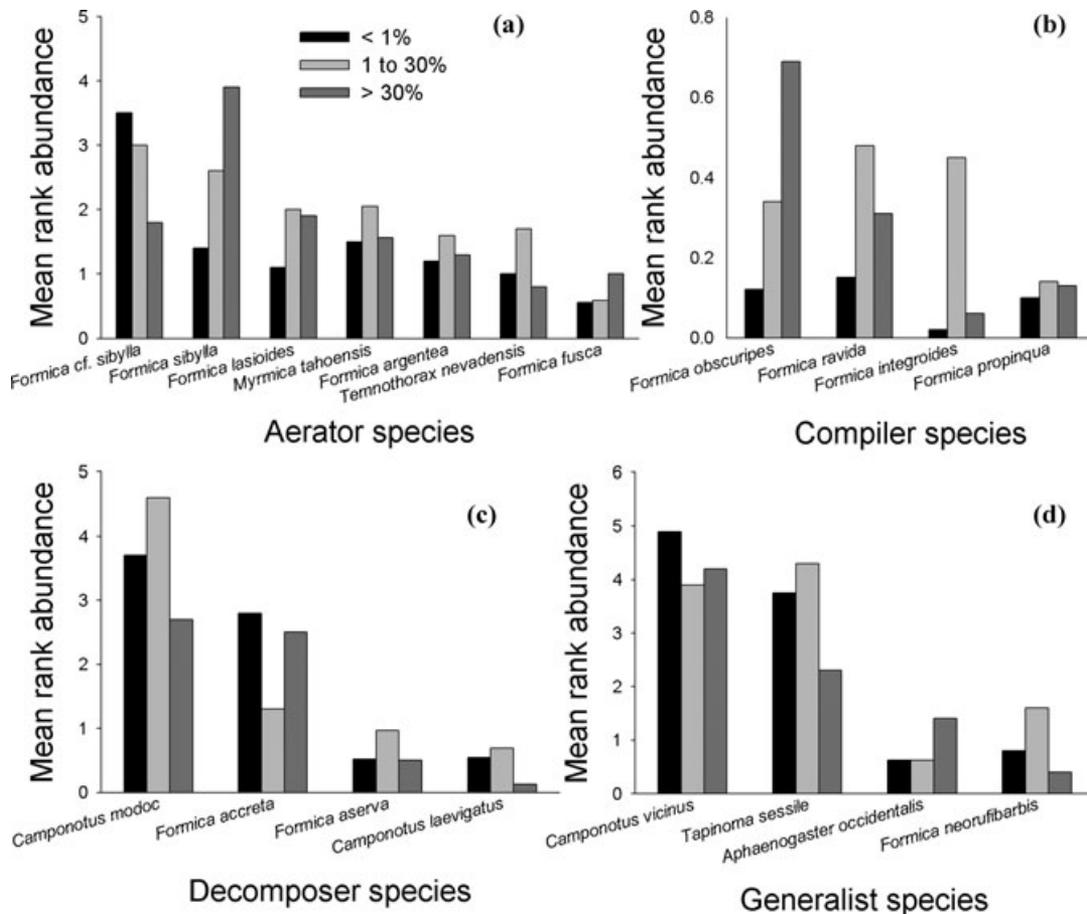


Figure 5. Patterns of abundance across 3 development categories (low, < 1% development; moderate, 1–30% development; high, > 30% development) of individual ant species within each of 3 service-providing units, (a) aerators, (b) decomposers, (c) compilers, and (d) generalists.

responding to the declines in coarse woody debris that are associated with higher levels of development in urban forests (Heckmann et al. 2008). This finding suggests that decomposer ants may be more resistant to increases in development where moderate densities of coarse woody debris are maintained.

The changes we observed in ant community composition in response to urban development and human use suggest concomitant impacts on the ecosystem services provided by ants. We observed compensatory shifts among species within all SPUs at lower levels of development (< 30%), above which even the more tolerant ant species declined as did the abundance of these service providers and the diversity of their responses. Although we did not directly measure ecosystem services, our results suggest that ecosystem services from native ecosystems can be readily affected by the status of the surrounding landscape. In the case of forested ecosystems, for example, ecosystem services include water quality, which can be affected by reduced water infiltration; wood production, which can be affected by reduced soil productivity and associated reductions in forest growth rates;

and fire safety, which can be affected by tree disease and mortality.

The aerator SPU responded most strongly to urban development, and aerator and compiler ants combined are likely to be the primary contributors to soil aeration in Lake Tahoe's forested ecosystems. Aerator ants contribute to water infiltration by increasing soil porosity from their subterranean tunnel networks (Lobry de Bruyn & Conacher 1994). Changes in abundance of aerator and compiler ants, or changes in densities and distribution of their nests, therefore may have substantial impacts on rates of water infiltration in montane forests. Relationships between land disturbance, ant diversity, and water infiltration in open spaces of interstitial forest have particular importance in the Lake Tahoe basin, where intensive efforts have been directed toward retaining and restoring water infiltration as a mechanism for improving water quality, most importantly toward the restoration of Lake Tahoe's famed clarity (e.g., Miller et al. 2006). Forested, undeveloped lands, regardless of their proximity to development or levels of human activity, are assumed to provide a "natural" level of water infiltration.

But, not surprisingly, no substantive attention has been paid to the ability of land parcels that have been acquired and protected from development to provide that desired ecosystem service.

Our findings substantiate the contention that ants respond to human disturbances (e.g., Kremen et al. 1993; Bestelmeyer & Wiens 1996; Bolger et al. 2000; Thompson & McLachlan 2007). They also suggest that metrics of ant biodiversity may be useful indicators of ecosystem conditions and services in management efforts on urbanizing and other disturbed landscapes. And, although our findings show that ant diversity declines dramatically at the highest levels urbanization and land disturbance, our results also indicate that intermediate levels of landscape conversion, including disturbances associated with forest management, can be compatible with diverse ant communities and the provision of ecosystem services by specialist ants.

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