Lakeshore Vegetation Effects on Avian and Anuran Populations

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ABSTRACT.—Riparian zones are hotspots of wildlife diversity and also particularly attractive for housing development. Landscaping associated with homes contributes to a wide range of lakeshore vegetation structures. Based on calling surveys in Northern Wisconsin, we investigated effects of lakeshore vegetation structure on bird diversity and frog abundance at three spatial scales: parcel (30 m of shoreline), whole-shore (340 m of shoreline) and whole-lake scales. For parcel and whole-shore scales, we selected sites paired by lake: 10 sites with an intact understory vegetation layer and 10 sites with a cleared understory. Green frog (*Rana clamitans*) abundances were somewhat related to presence of forest understory at the parcel scale. More clearly, we found higher avian species richness at sites with intact understory vegetation than those without, and increasing richness with canopy coverage. Aerial insect abundances, which were also higher at sites with an intact understory, may help explain bird distributions. Our results suggest that riparian understory landscaping at the scale of individual parcels can alter local bird communities.

INTRODUCTION

Housing densities have increased in many rural areas with scenic amenities such as mountains and lakes, making it increasingly important to understand the implications of low-density residential development on native biota (Hansen *et al.*, 2005; Radeloff *et al.*, 2005). Development within riparian zones warrants particular attention because these areas are biodiversity hotspots (Burger, 2000; Decamps *et al.*, 2004). In addition to supporting amphibian species, riparian areas support higher bird diversity and abundance than adjacent uplands (LaRue *et al.*, 1995; Dobrowolski, 1997; Whitaker *et al.*, 2000; Macdonald *et al.*, 2006). Riparian ecosystems in northern Wisconsin face unprecedented ecological stress due to housing growth (Wisconsin Department of Natural Resources, 1996). Residential development can indirectly reduce wildlife populations by reducing habitat quality. Avian diversity, small mammal diversity and green frog densities may be lower around lakes with higher development levels (Robertson and Flood, 1980; Racey and Euler, 1982; Woodford and Meyer, 2003; but *see* Clark *et al.*, 1984).

Although many factors contribute to declining habitat quality around housing developments (*e.g.*, King and Balogh, 2001; Maestas *et al.*, 2003; Hansen *et al.*, 2005), simplification of vegetation structure may be the primary driver of lakeshore wildlife community changes (Racey and Euler, 1983; Clark *et al.*, 1984; Elias and Meyer, 2003). Riparian property owners often leave the canopy intact, but remove or trim understory plants (Racey and Euler, 1983; Clark *et al.*, 1984; Elias and Meyer, 2003; but *see* Lindsay *et al.*, 2002). Because some riparian homeowners maintain extensive natural shoreline vegetation while others create well-trimmed lawns confined by sea walls, we expected vegetation structure to be a better descriptor of wildlife habitat quality than building density. We investigated how insect abundance and two measures of vegetation structure - presence of understory vegetation (any plants 0.2–2 m high) and canopy cover index – affect bird and frog communities in forested lakeshore environments.

Despite evidence that organisms respond differently to their environments at different spatial scales (*e.g.*, Addicott *et al.*, 1987; Wiens, 1989; Orians and Wittenberger, 1991; Luck,

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2002; Bossenbroek *et al.*, 2004), previous lakeshore research on birds and frogs has been restricted to the whole-lake scale. We investigated the riparian environment for birds at parcel- (30 m) and whole-lake (mean perimeter 9000 m) scales because these are the spatial extents at which riparian management decisions are often made. For frogs, we also considered shoreline lengths of 340 m. Information about how lakeshore vegetation structure affects wildlife at different spatial scales should help in making informed shoreline zoning and riparian buffer laws.

Birds can be used as bioindicators to monitor changes in the species richness of an area (Fleishman *et al.*, 2005). Because of avian mobility in habitat selection, altered bird communities may be among the first ecological responses to reduced riparian vegetation structure. Avian ecologists have long understood that bird diversity (*e.g.*, MacArthur and MacAuthur, 1961; Cody, 1981; Bersier and Meyer, 1995) and density (Niemi and Hanowski, 1984; Freemark and Merriam, 1986; Probst *et al.*, 1992; Hurlbert, 2004) are linked to vegetation structure. Vegetation structure in the canopy and understory provides birds with nesting sites, perches, predator refuges and foraging substrates (Cody, 1981), which led us to expect higher avian richness at sites with greater vegetation structure.

Frogs can also be useful indicators of changing riparian ecosystems (Welsh and Ollivier, 1998), although they are susceptible to changes in both their terrestrial and aquatic environments (Hero *et al.*, 2005). Terrestrial amphibian habitat alteration, which changes ambient temperatures, soil moisture, and prey, may be one underlying cause of amphibian declines (Lindler *et al.*, 2003). Frog abundance and richness increase with forest cover (Hecnar and M'Closkey, 1998; Knutson *et al.*, 1999) and riparian understory cover (Courtois *et al.*, 1995). Woodford and Meyer (2003) propose that the negative correlation they observed between green frog (*Rana clamitans*) abundance at the whole-lake scale and lakeshore building density resulted from losses of riparian wetland plants and emergent plants in shallow water. Reduced vegetation structure diminishes refuge from predators during the calling season (Wells, 1977; Walsh and Downie, 2005), leading us to expect lower frog abundances at sites with cleared understory vegetation.

METHODS

STUDY AREA

We conducted this study in Vilas County in northeastern Wisconsin, USA, in the center of the Northern Highlands Lake District (*see* Peterson *et al.*, 2003 for more details on NHLD). The landscape is forested, having a high density of glacial lakes (over 1300 lakes in the 2639 km^2 county) and residential development that is concentrated around the lakes (Schnaiberg *et al.*, 2002). Curtis (1959) classified the vegetation as northern wet forest and boreal forest. The majority of our study sites were privately owned; 14% were public property.

Site and lake characteristics.—On each of 10 randomly chosen lakes, we selected one site with intact understory vegetation and paired it with a site cleared of understory vegetation. We chose paired sites similar in aspect, fetch, slope, littoral macrophyte density and hydrologic context. Paired sites on the same lake were separated by at least 200 m, and the lake sites were separated by at least 6.5 km. The 30 m water frontage length of each site reflects that of most Vilas County lakeshore parcels sold in 1997–2001 (mode = 30.5 m; median = 42.1 m, B. Provencher, University of Wisconsin- Madison, unpubl. data). Proportion of the site shoreline with adjacent aquatic macrophytes was generally low (mean = 0.16, SD = 0.29). We defined riparian understory vegetation as any foliage 0.2–2 m above the ground and within 5 m of the water's edge (Fig. 1). The 10 sites with cleared understory
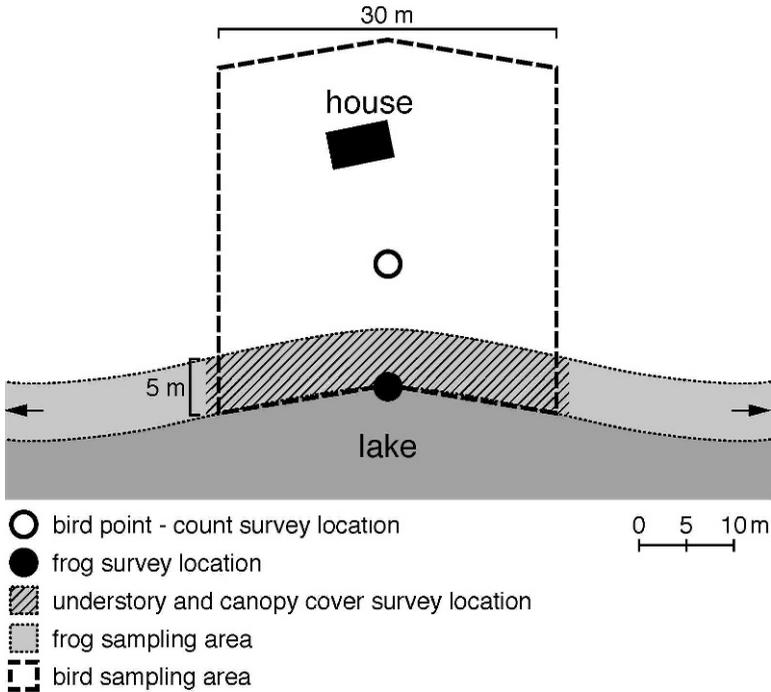
FIG. 1.—Layout of one parcel-sized site (20 total, paired by lake), illustrating relative positions of vegetation, bird and frog sampling areas. Frog surveys consisted of calling intensity index estimates within the "audible calling range," which included the 340 m of shoreline around each study location

vegetation had manicured lawns with no shrubs, saplings, wetland sedges or other tall understory vegetation; two had sea walls. A house was often, but not always, immediately adjacent to the cleared understory sites. The 10 sites with intact understory vegetation had a dense layer of shrubs (mainly *Alnus rugosa*), saplings (*e.g.*, *Betula papyrifera*, *Thuja occidentalis*, *Acer rubrum*) or wetland plants (*e.g.*, *Carex retrorsa*, *Juncus effusus*, *Sparganium spp.*). Three of these sites also had houses present.

We visually classified the area of canopy cover above 3 m in height for each 30 × 5 m site (Fig. 1) according to the following index: none, sparse (10–40%), partial (40–70%) or full (70–100%) cover. The sites with intact understory vegetation had either full (8 sites) or partial (2 sites) canopies; sites with cleared understory included the whole range of canopy categories (1full, 4 partial, 4 sparse, 1 no canopy).

We also recorded percent of cleared riparian understory from a wider shoreline around the parcel-size sites because surveys included the entire audible range of a calling green frog (*see* Frog Surveys, below). We measured the audible frog calling range by locating an isolated, frequently calling green frog on the lakeshore from a boat and moving away to record the distance at which the frog could no longer be heard. We repeated this at five locations to find an average audible frog calling range of 336 m (SD ± 76 m). Therefore, our measure of cleared shorelines was based on 340 m of shoreline, centered at the middle of each 30-m site (Fig. 1). Within this audible frog calling range, proportion of cleared shoreline ranged from 0% to 52%.

We estimated the proportion of entire lake perimeters with a cleared understory. We did this by recording cleared understory lengths by boat with a Global Positioning System (GPS) unit and ArcGIS 9 software (Version 9.1, 2005 ESRI Inc., Redland, CA). Proportion of lakeshores with cleared understory vegetation ranged from 2.7% to 24.7%.

Insect Sampling.—We estimated relative aerial insect abundances at the center of each paired site using sticky traps. We stapled yellow 7.6 × 12.7 cm cards covered on both sides with nontoxic glue (Tanglefoot, Grand Rapids, MI) atop 1 m-high wooden stakes and posted them 5 m inland from the shoreline (Hoback *et al.*, 1999). We removed traps from each site after about 1 wk (with exact times paired by lake). We repeated this consecutively three times at each site between 3 Jun. and 7 Jul. 2005.

Bird Surveys.—We recorded estimates of bird species richness at each site on three mornings between 0500 and 1000 CST. Bird point counts took place between 27 May and 28 Jun. 2005 on calm days with no precipitation. We typically visited four sites per morning, with site visits staggered to ensure similar distributions of early and late morning surveys at each site. We conducted auditory point counts while standing 8 to 22 m inland from the water (Fig. 1). We maintained equal distances from the water for each pair of sites, but distance depended on house location (when houses were present). After a 2 min quiet period, we recorded presence or absence of species based on singing males heard within the 30 × 30 m sampling area during a 20-min period. We did not count flyovers, shorebirds (Charadriiformes), waterfowl or birds that were clearly audible from outside the sampling area. Birds and frogs were both surveyed three times at all 20 sites; we completed the first round of point count surveys (all sites on all lakes) before the next round began.

Frog Surveys.—We conducted frog calling surveys three times at each site on evenings in Jul. 2005, beginning 30 min after sunset. This survey period captured the peak mating season for green frogs (*Rana clamitans melanota*) and bullfrogs (*R. catesbeiana*) in northern Wisconsin. All surveys occurred on evenings with very little wind, no precipitation and temperatures above 10 C (Mossman and Hine, 1984). We completed four site surveys per night, staggering the order of site visits to ensure similar distributions of survey times. After a 2 min quiet period, we estimated abundance of calling frog species heard in a 10 min period from the shoreline at the center of the site. Frog abundance was based on intensity of frog calls using a calling index method: 0 = no calls heard; 1 = individual calls heard infrequently; 2 = individual calls heard frequently; 3 = frequent calling with some overlap; 4 = continuous overlapping calls (Nelson and Graves, 2004).

Data Analyses.—We compared bird communities among sites with and without the understory using the blocked multi-response permutation procedure available in PC-ORD, version 4.33 (blocked MRPP; Mielke 1984; MjM Software Design, Gleneden Beach, OR, USA). Using median alignment and blocking by lake, this test estimates the probability of an observed difference between sites occurring by chance. The MRPP procedure also calculates a within-group agreement statistic, A, which describes the observed within-group (*e.g.*, all intact understory sites) homogeneity compared with random expectation. When all plots within a treatment group have identical community compositions, A = 1; when within-group heterogeneity equals that expected by random chance (*i.e.*, no 'effect' of treatments), A = 0. Values of A between 0.1 and 0.3 often indicate meaningful similarities in ecological communities (McCune and Grace, 2002). Blocked MRPP tests can only use the Euclidean distance measure, so we also calculated the Sorensen (Bray-Curtis) coefficient of similarity for bird communities paired by lake (Bray and Curtis, 1957).

We categorized birds into overlapping guilds based on urban versus woodland habitat preference, diet, and nesting habit (De Graaf *et al.*, 1985; Peterjohn and Sauer, 1993). We

compared total avian richness (number of species present), within-guild richness (number of species within each of the guilds) and species occurrence (number of days out of three survey dates the species was present) between intact understory sites and cleared understory sites. To test null hypotheses that bird species richness, species occurrence and insect abundance do not differ between intact and cleared understory sites, we used the Wilcoxon signed ranks test, with sites paired by lake (Conover, 1971). Conducting insect, bird and frog surveys at both sites on the same lakes during the same dates removed temporal effects from our analyses testing understory effects. We tested canopy cover effects on within-guild richness using separate mixed effects linear regressions because canopy and understory categories were not completely independent of each other. The random effects term accounted for non-independence of sites on the same lakes. We excluded the single site with no canopy cover from these analyses. After finding significant effects of canopy as an ordered categorical variable, we assessed differences between canopy categories using Bonferroni-corrected *t*-tests. Using mixed effects multiple linear regressions, we evaluated how site insect abundance (square-root-transformed) plus understory category relates to bird richness and within-guild richness. We also used mixed effects multiple linear regression to evaluate the relationship between bird richness and bird feeder presence plus understory category.

At the lake scale, we regressed bird richness and frog abundances on proportion of the entire lakeshore cleared of understory vegetation. We also tested whether green frog and bullfrog calling intensity related to parcel understory and canopy categories or whole-shore (calling range) understory vegetation abundance using mixed effects linear regressions with lake as the random effect. We completed all statistical tests other than the multivariate analyses using R software (R Development Core Team 2006, Vienna, Austria). We used a significance level of $P < 0.05$, but also reported all non-significant p-values less than 0.1.

RESULTS

BIRD RESPONSE

Bird community composition differed with presence or absence of the understory layer at the parcel scale (MRPP $T = -4.00$, $P < 0.001$, mean Sorensen coefficient = 0.36, SD = 0.07). However, the assemblages of species present at intact understory sites and cleared understory sites were not very consistent among lakes (A = 0.05). Seven of the 62 bird species occurred more frequently at sites with intact understory vegetation than at sites with a cleared understory, while none occurred significantly more frequently at the cleared understory vegetation sites (Table 1).

We found higher bird species richness at intact understory sites (Table 2) and at those with full canopy cover than at sites with sparse or partial cover ($F_{2,7} = 7.4$, $P = 0.02$; Fig. 2). Four of the five guilds examined had higher within-guild species richness at intact understory sites than at cleared understory sites (Table 2). Sites with full canopies also had higher within-guild species richness for three of the five guilds than sites with sparse or partial canopy cover (woodland species: $F_{3,6} = 10.1$, $P = 0.009$; mid-story and canopy nesting species: $F_{2,7} = 4.7$, $P = 0.05$; insectivorous species: $F = 5.6$, $P = 0.035$; Fig. 2). Presence of bird feeders (at nine sites) did not help explain total avian richness at our sites. We found no relationship between whole-lake proportion intact understory and avian richness.

Variation in insects trapped was greatest among cleared understory sites, but mean insect abundance during 1 wk periods was greater at intact understory sites ($\bar{x} = 241.8$, SE = 26.9) than at cleared understory sites ($\bar{x} = 191.7$, SE = 37.1; Wilcoxon $T = 100$, $P < 0.001$). Insect

TABLE 1.—Bird species exhibiting differences in mean frequency of occurrence (number of days detected out of three) from 10 sites with and without riparian understory vegetation. Frequency of occurrence differences between sites with and without understory vegetation were not significant (p-value < 0.1) for the other 54 species observed at these sites in Wisconsin, USA

Bird species	Occurrence at cleared understory		Occurrence at intact understory		Wilcoxon T value	p-value
	Mean	SE	Mean	SE		
Red-eyed vireo *Vireo olivaceus*	0.6	0.2	1.6	0.3	19	0.015
Blue-headed vireo *Vireo solitarius*	0	0	0.6	0.2	25	0.014
Northern parula *Parula americana*	0	0	0.5	0.2	25	0.014
Black-throated green warbler *Dendroica virens*	0	0	0.4	0.2	30	0.033
Palm warbler *Dendroica palmarum*	0.1	0.1	0.8	0.1	15	0.002
Pine warbler *Dendroica pinus*	0.1	0.1	1.2	0.3	18	0.007
Ovenbird *Seiurus aurocapilla*	0	0	0.7	0.3	30	0.034

abundance was not related to canopy cover index. Multiple linear regressions that first took understory category into account resulted in only a weak positive effect of insect abundance on total bird species richness (t = 2.3, df = 8, P = 0.05), but not on within-guild richness.

FROG RESPONSE

Mean calling index ranged from 0 to 2.67 for both anuran species. We found no significant relationships between green frog or bullfrog abundances and proportion of understory vegetation at the calling-range or whole-lake scales. Green frogs were slightly more abundant at parcel-size sites with understory vegetation (calling index mean = 2.2, SE = 0.3) than at sites with a cleared understory (calling index mean = 1.5, SE = 0.3; mixed-effects regression $F_{1,9}$ = 4.4, P = 0.07).

DISCUSSION

Our finding that bird communities varied with understory structure offers one explanation for why housing development alters bird community composition (Robertson and Flood, 1980; Clark *et al.*, 1984; Friesen *et al.*, 1995; Lindsay *et al.*, 2002). Absence of higher urban species occurrence or richness at sites with a sparse canopy or cleared understory contrasts somewhat with previous studies (Clark *et al.*, 1984; Lindsay *et al.*, 2002), although the survey scales differed. Similar to other north-temperate lakeshore studies that

TABLE 2.—Mean number of bird species detected within functional guilds at Wisconsin lakeshores in 2005: 10 sites with a cleared understory and 10 sites with an intact understory

| | Species richness | | | | | |
| | Cleared understory | | Intact understory | | | |
Avian groups	Mean	SE	Mean	SE	Wilcoxon T value	P-value
All species	10.1	0.7	15.8	0.9	4.5	<0.001
Nesting Guilds						
Ground & Low	1.1	0.2	3.1	0.7	18	0.013
Midstory & Canopy	7.3	0.6	10.3	0.6	2	<0.001
Habitat Guilds						
Woodland	3.7	0.3	7.2	0.5	3.5	<0.001
Urban	2.2	0.2	1.9	0.3	60	0.42
Diet Guild						
Insectivore	5.3	0.6	10.2	0.8	3.5	<0.001

considered whole-lake building densities (Robertson and Flood, 1980; Lindsay *et al.*, 2002), we found no relationships between whole-lake proportion of understory vegetation and avian richness. However, investigation at the parcel scale led to a clearer predictor of avian species richness.

The primary results are consistent with the general rule that increased vegetation complexity results in higher avian diversity. Use of dense foliage for refuge, nesting or foraging likely accounts for higher species richness at sites with understory vegetation and dense canopies. Low community similarity among the 10 sites with the same understory category may reflect staggered survey dates among lakes, or other environmental variables such as canopy cover. A fully crossed study could help isolate canopy from understory vegetation effects.

Higher insect abundances at intact understory sites than at cleared sites may help explain higher bird diversity at these sites, although the correlation between these two predictor variables obscured effects of insects alone. Swarms of aerial insects lead to notoriously variable spatial distributions, as we found with extremely high insect abundances at one outlier site lacking understory cover. Previous studies indicate higher insect and spider abundances in areas with more complex vegetation structure (Halaj *et al.*, 1998, Langellotto and Denno, 2004), but few studies have considered effects of vegetation structure on abundance of aerial insects (Halaj *et al.*, 2000).

The weak relationship observed between frog abundance and understory structure differs from Woodford and Meyer's (2003) findings on similar Wisconsin lakes, possibly due to different survey protocols. Whereas Woodford and Meyer (2003) surveyed frog abundance around the entire lake (using a similar but coarser calling index) and related it to a measure of whole-lake riparian vegetation, we surveyed frog calls from two locations per lake and related it to vegetation at three different scales. Green frogs select mating territories based on riparian vegetation cover, water depth and aquatic vegetation (Wells, 1977), so riparian vegetation effects are likely only detectable if aquatic depth and vegetation requirements are met.

This study supports the protection or restoration of riparian vegetation buffers for avian species richness, specifically at a fine spatial scale (30 m of shoreline by 5 m inland). Irrespective of housing density, shoreline landscaping on individual parcels can result in lakes with highly variable riparian vegetation structure. Thus, landscaping modifications to the riparian understory or canopy made by individual property owners can alter local bird
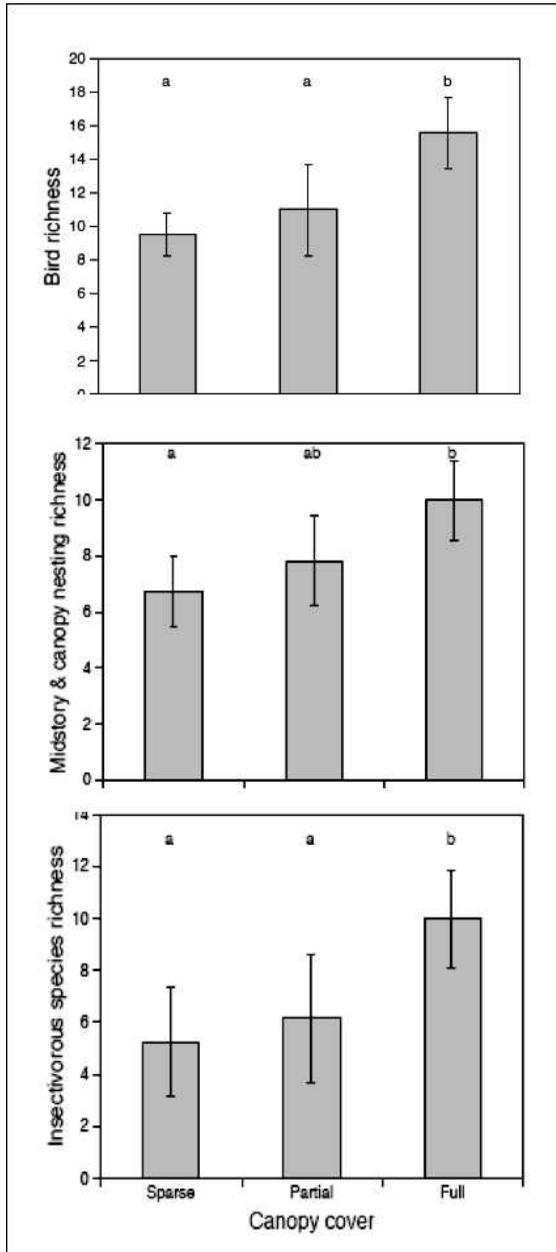
FIG. 2.—Mean species richness (±2 SE) of birds in three categories (A. total species, B. mid-story and canopy nesting guild, C. insectivore guild) under varying levels of riparian canopy cover (n = 19 sites) on Wisconsin lakes in 2005. Different letters indicate significant differences (within guilds) among canopy cover categories, based on mixed-effects ANOVA ($P < 0.05$; model included a random effect term for sites on same lakes)

species richness. Riparian buffer restoration that increases densities of native understory plants will likely increase local bird diversity. However, to test whether riparian buffers serve as viable wildlife habitat rather than ecological traps (environments attractive to the animals, but actually population sinks), we need field experiments that include detailed wildlife demographics.

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