How much city is too much city? Biodiversity and ecosystem functioning along an urban gradient

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How much city is too much city? Biodiversity and ecosystem functioning along an urban gradient

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Summary

1. Over half of the world’s population resides in urban areas, a huge proportion of which occur along the coast. As cities expand, the ability of coastal ecosystems to provide the services people need from them is in question. While it is well understood that coastal development changes ecosystems, a quantitative understanding of such relationships across the land-sea boundary is generally lacking.

2. We investigated how land cover—a potential indicator of stressors such as toxic contaminants, nutrient loads, and extractive uses—related to empirically measured ecosystem properties in freshwater (stream) and marine (intertidal) habitats in the Puget Sound region of WA, USA. Specifically, we estimated how biodiversity (macroinvertebrate family density and Simpson diversity), benthic net primary productivity, and decomposition varied across six pairs of more and less urbanized, coastal watersheds.

3. While freshwater biodiversity and marine primary productivity were significantly lower in more urbanized watersheds, marine biodiversity, freshwater primary productivity, and freshwater and marine decomposition rates were not significantly different among watershed pairs.

4. Some watershed pairs differed more in the extent of urbanization than others, and greater differences in imperviousness between watershed pairs were associated with greater reductions in stream biodiversity in more urbanized watersheds. In contrast and surprisingly, however, watershed pairs that were most different in imperviousness tended to be least different in marine biodiversity.
5. We found no evidence that associations between biodiversity, ecosystem functions, and urbanization attenuated from freshwater to marine habitats, as might be expected if the land-sea boundary diminished effects of terrestrial development.

6. Synthesis and applications. These results add support to growing evidence that a dichotomy between urbanized and non-urbanized ecological communities may be less straightforward than is often assumed, and reinforce the idea that true ecosystem-level management requires integrated land-sea planning. Thus, our study suggests that conservation attention focused singularly on remote and relatively untouched places is necessary but not sufficient in the Anthropocene. Similarly, this work implies that jurisdictionally convenient but ecologically unjustified attention to terrestrial, freshwater, or marine systems in isolation cannot be considered true ecosystem-based management.

Key-words: land-sea, ecosystem structure, ecosystem function, biodiversity, urban gradient


Introduction

Despite comprising ~2% of the global land surface, urban areas are home to more than half of the world’s population (UN 2014). In the US, 30-50% of people live in coastal counties, primarily in cities (Crossett et al. 2013). Coastal cities are experiencing especially rapid change, with urban expansion directly drawing down natural resources, consuming undeveloped and agricultural lands, and influencing biodiversity and ecosystem functions (Buller & Chapman 2010, SCBD 2012). While it is well understood that coastal development changes natural ecosystems, a quantitative understanding of the relationship between development and ecosystem function is generally lacking (but see McClelland et al. 1997, Koch et al. 2009).

A robust understanding of how urbanization alters ecosystems, and what conservation value remains within urban areas, is timely. Coastal cities concentrate many social benefits for people because they serve as cultural hubs and centers of commerce and trade (Ernstson et al. 2010), and there is increasing appreciation that they are also places that nature’s benefits are most needed (Granek et al. 2010). For example, there is growing demand for natural vegetation and structures that improve freshwater quality for both consumption and recreational purposes (e.g., McIntyre et al. 2015), provide coastal protection from storms and sea level rise (Koch et al. 2009, Arkema et al. 2013), and serve as nursery habitat for fishery and protected species (Beck et al. 2001). Meeting this demand will require a rigorous scientific understanding of how urban development changes ecosystem structure and function relative to other local, regional, and global influences (Halpern et al. 2009, Alvarez-Romero et al. 2011).
The literature is replete with hypotheses about processes associated with urban land development that modify ecosystem structure and function (Table 1). These processes include increases in: species introductions, nutrient inputs, stream flow, sediment runoff, water temperature, low-oxygen areas, toxic contaminants, and extractive use. Often these hypotheses imply, directly or indirectly, that the effects of development should be strongest on land, and attenuate but not necessarily extinguish in coastal marine ecosystems (Alvarez-Romero et al. 2011). In some cases, it is clear that the influence of terrestrial inputs, such as dissolved organic carbon, are diminished in aquatic systems, but such findings remain a contentious area of investigation (Brett et al. 2009). Quantitative evidence for specific urban impacts on ecosystem structure and function is beginning to emerge (Cuffney et al. 2010), though few published studies consider the extent to which urbanization effects are linked across land-sea boundaries (Stoms et al. 2005, Alberti et al. 2007, Tallis et al. 2008, Beger et al. 2010).

Here, we test the hypothesis that ecosystem structure and function (hereafter, ecosystem properties) of freshwater and nearshore marine habitats are strongly associated with the extent of adjacent urbanization. We examine habitats in the region of Puget Sound, WA, USA, an area of burgeoning population growth (PSRC 2015) with strong land-sea connections. We investigate whether two measures of biodiversity and two types of ecosystem functions in freshwater and marine habitats: (i) differ systematically between more and less urbanized areas, with the expectation that more urbanized areas would exhibit lower diversity and ecosystem functioning; and (ii) display equally strong associations with urbanization, anticipating that relationships with urban land use are stronger in freshwater than marine habitats.
Materials and Methods

Study region

The Puget Sound region includes the lands and waters from the crests of the Cascade and Olympic mountains to the marine waters as far south as Olympia, WA, north to the San Juan Islands and west to the mouth of the Strait of Juan de Fuca (Ruckelshaus and McClure 2007; Fig. 1). Puget Sound itself is typically divided into 7 oceanographic basins based on physical and chemical properties (Simenstad et al. 2011). The region is characterized by a full range of coastal land cover, from undeveloped to intensely developed including uninhabited wilderness areas, three national parks, and densely populated cities (0-232 people km\(^{-2}\), including the metropolitan hubs of Seattle and Tacoma). These features make this coastal region an excellent test bed for understanding how ecosystem properties change along an urban gradient.

Characterizing variability in urbanization and ecosystem properties: defining the urban gradient

We quantified watershed scale patterns of urbanization in streams that flowed directly into Puget Sound using ESRI ArcGIS software suite (v.10.1). We used an existing river basin geospatial data layer (PSNERP 2010) to select watersheds that were ≤1,000 ha, and contained ephemeral and perennial streams (USEPA & USGS 2005). Using watersheds that met these criteria, we considered four different geospatial data layers that captured alternative aspects of urbanization: imperviousness (i.e., surface areas that reduce infiltration and increase runoff; Schueler et al. 2009), roadways...
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(OpenStreetMap 2012), land use and land cover (LULC, Fry et al. 2006), and shoreline armoring (PSNERP 2010). For the continuous data layers (imperviousness and roadways) we calculated area weighted mean values for each watershed. For the categorical data layers (LULC, shoreline armoring), we calculated the proportion of each watershed that was classified as developed as well as the proportion of the associated shoreline that was armored.

To characterize the rural-to-urban gradient, we reduced the dimensionality of the four land cover data layers using principal components analysis (PCA) in Primer v6. This approach also reduced the likelihood of confounding the relationship between data layers used to generate the urban gradient a priori and covariates used to explore correlations with our response variables post hoc (Alberti 2008, Spirandelli 2014). Prior to the PCA, we normalized the data layers to ensure that they were equally influential in describing the urban gradient. The first two principal components (PC1 and PC2) explained 92% of the among-watershed variation in the original four LULC data layers (Table S1; Fig. 1a). Increasingly positive values of PC1 (74%) corresponded to more human-modified watersheds (specifically, those with greater imperviousness, road, and developed land cover). Increasingly positive values of PC2 (18%) corresponded primarily to increased armoring, after accounting for effects of imperviousness.

Characterizing variability in urbanization and ecosystem properties: study design

In order to account for well-known spatial variability in both abiotic (e.g., salinity) and biotic (e.g., recruitment) factors (Dethier et al. 2012), we collected data from six pairs of watersheds characterized by perennial streams, with similar drainage areas,
occurring at similar latitudes, within the same oceanographic basins (5 pairs within Central Puget Sound, 1 pair in Hood Canal), and spanning a wide range of urbanization across Puget Sound (Fig. 1b, Table S2). Each pair consisted of a more and less urbanized watershed, such that more urbanized watersheds were defined as those that were more anthropogenically-modified (i.e., higher PC1 and PC2 scores). Nested within each watershed, we selected two study sites, one each in freshwater and nearshore marine habitats. This paired-watershed study design allowed us to test for an association of urbanization with ecosystem properties in freshwater and marine habitats, while controlling for as many other factors as possible.

Our study focused on biodiversity and two types of ecosystem functions—net primary productivity and decomposition. Changes in biodiversity are a primary concern related to urbanization (Pickett et al. 1997, Aronson et al. 2014, Beninde et al. 2015, Clark et al. 2015). We evaluated two measures of biodiversity, the number of benthic macroinvertebrate families (family density), and the distribution of individuals among these families (Simpson diversity). Benthic macroinvertebrates have long been considered useful indicator species in both freshwater (Morley and Karr 2002) and marine (Bilkovic et al. 2006) habitats because they are relatively sedentary and tend to respond quickly to changes in local environmental conditions. Net primary productivity and decomposition are two ecosystem functions thought to respond directly to urbanization, via associated changes in abiotic factors such as light and flow, or indirectly via changes in ecological communities (Table 1). These functions are fundamental to the production of new biomass and cycling of energy in ecosystems (Vitousek 1986, Cebrián and Lartigue 2004).
Characterizing variability in urbanization and ecosystem properties: biodiversity

In marine habitats, we collected epibenthic macroinvertebrates along an ~100 m length of coastline at each of the study sites (n=3 samples site\(^{-1}\)). Collections occurred in July 2012, 2013, and 2014 using a benthic sled (1 m x 1 m opening, 1 mm mesh), towed over 10 m transects at each site (~0.5m tidal elevation). We sampled the epibenthic community occurring within eelgrass beds (except for 3 sites in which eelgrass did not occur; Table S2), and samples were stored on ice in the field and transferred to ethanol for preservation within 24 hours.

In freshwater habitats, we leveraged existing long-term data on stream invertebrates around Puget Sound (Puget Sound Stream Benthos 2015). To ensure temporal comparability between marine and freshwater habitats, we focused on stream macroinvertebrate data collected by a variety of regional agencies and environmental organizations between 2012-2013 in the South Central Basin of Puget Sound (for detailed methods, see King County 2009). Our analyses relied on count data aggregated at the family level to maximize the number of database entries we could use (n=37 watersheds ≤1,000 ha with perennial streams flowing directly into Puget Sound) and to ensure consistency with analysis of invertebrate data we collected from marine habitats. We examined all possible pairings of more and less urbanized watersheds contained within this database, where urbanization was defined using the PCA described above.

For both marine and freshwater habitats, we quantified the number of macroinvertebrates in each taxonomic family (Table S3, S4), a resolution considered sufficient for capturing spatial differences in species composition for this region (Dethier
and Schoch 2006, Morley and Karr 2002). We used the observed number of invertebrate families to estimate family density (number of taxonomic families observed) and Simpson diversity (a measure of evenness) from each sample (with the vegan package in R v3.1; Oksanen et al. 2015, R Core Team 2014).

Characterizing variability in urbanization and ecosystem properties: net primary productivity

We assayed benthic freshwater and marine net primary productivity by tracking algal growth on pre-rinsed unglazed ceramic tiles (10cm x 10cm x 0.5cm deep; n = 10 site\textsuperscript{-1}) in June-August 2012-2013. In marine habitats, we used plastic ties to attach tiles to the tops of 1m long vertical PVC poles spaced evenly along an ~100m length of coastline (~0.5m tidal elevation). In the freshwater habitats, we placed tiles exclusively in riffles every 2-5 m along a 100-200m reach. Tiles were attached to hardware cloth using plastic ties, and hardware cloth was attached to the streambed using rebar. We collected tiles from both freshwater and marine habitats after 8-12 weeks to determine algal biomass accrual.

Algal growth in streams was exclusively micro-algal (e.g. benthic diatoms) while marine production was dominated by macroalgae such as Ulva spp. Tiles were stored on ice in the field and processed in the lab within 24 hours.

Prior to processing, we rinsed the tiles of sediments and removed macroinvertebrates visible to the naked eye to minimize overestimation of algal organic matter. We scrubbed algae from the top surface of each tile using a bristled brush and filtered water. For marine tiles, algal scrapings were placed directly into aluminum weigh boats, dried at 60°C for ≥72 hours, weighed, ashed at 400°C for 2 hours, and reweighed (Hixon and
Brostoff 1996). For freshwater tiles, twenty percent of the resulting 500 mL slurry was filtered onto a pre-ashed, pre-weighed 47-mm GF/F filter. These samples were dried at 60°C for 24 hours, weighed, ashed at 400°C for 2 hours, and reweighed (Steinman et al. 2007). For both freshwater and marine tiles, the ash-free dry mass (AFDM) was taken as an estimate of the organic content of algae present on the tiles at the time of collection. We divided this measure of organic content by the amount of time the tiles were deployed to estimate rates of net primary productivity. (Preliminary investigation of tiles collected after 14, 28, 60, 90, and 120 days during a separate 2012 study suggested a linear rate of algal increase over time; Samhouri et al. unpublished data).

Characterizing variability in urbanization and ecosystem properties: decomposition

To track litter decomposition, we collected freshly fallen, dried maple leaves (Acer spp; freshwater habitats) or rinsed, drift eelgrass (Zostera marina; marine habitats) and deployed these materials in mesh litter bags at each site (n = 8, 10 g bags site⁻¹). In the marine habitats, we used plastic ties to attach litter bags to the tops of 1 m long vertical PVC poles spaced evenly along an ~100 m length of coastline in August 2013 (~0.5 m tidal elevation). In the freshwater habitats, we placed the litter bags exclusively in riffles every 2 m -10 m along a 100-200 m reach in early November 2012 and 2013. Litter bags were attached to rebar (embedded within the streams) using plastic ties. We collected litter bags from both freshwater (1-2 months later) and marine (4-6 weeks later) habitats to determine litter loss rates. Litter bags were stored on ice in the field and processed in the lab within 24 hours.
Prior to processing, we rinsed the litter bags of sediments and removed macroinvertebrates visible to the naked eye to minimize overestimation of remaining organic matter. These pre-processed samples were transferred to aluminum weigh boats and dried at 60°C to constant weight for 24-72 hours, weighed, ashed at 400°C for 2 hours, and reweighed (Bretherton et al. 2011, Nicastro et al. 2012). For both freshwater and marine litter bags, the ash-free dry mass (AFDM) was taken as an estimate of the organic content of litter remaining at the time of collection. Decomposition rates were estimated as the difference between initial litter bag weights (10g) and organic content remaining at the time of collection, divided by the number of days the litters bags were deployed.

Characterizing variability in urbanization and ecosystem properties: other environmental characteristics

We measured several other environmental characteristics that may be associated with the ecosystem properties described above (Table 2 and Supporting Information). We estimated an average for each of the environmental characteristics at all of our study sites.

Analyses: categorical comparisons between more and less urbanized watersheds

Our primary hypothesis was that differences in four ecosystem properties (family density, Simpson diversity, net primary productivity, and decomposition) in marine and freshwater habitats would be associated with the extent of urbanization in the surrounding watersheds. We analyzed our data in two ways. First, we considered categorical
differences in urbanization (more vs. less urbanized) between watershed pairs. Specifically, we conducted a paired t-test for each of the ecosystem properties in each habitat to evaluate the null hypothesis of no difference between more and less urbanized watersheds.

Analyses: comparisons of ecosystem properties along a continuum of urbanization

Because urbanization scores for some watershed pairs differed more widely than for others (Fig. 1b; e.g., compare Pair 3 with Pair 6), we also examined pairwise differences in ecosystem properties within each watershed pair. Because imperviousness loaded more strongly than any other data layer on PC1 (Table A1), we estimated the disparity in urbanization as the difference in imperviousness between the more and less urbanized watershed in each pair (hereafter, impervious distance). Similarly, to estimate the disparity in ecosystem properties, we calculated the difference in the average value of each property between the more and less urbanized watershed in each pair (hereafter, ecosystem property distance). We used ANCOVA to test for an effect on ecosystem property distance (e.g., Simpson diversity distance) of impervious distance (a linear covariate) and year (a categorical factor), along with their interaction. We used post hoc pooling procedures to sequentially remove non-significant interactions terms, beginning with the highest order interactions (Winer et al. 1991). This analytical structure accurately reflected the paired design of our study and thus provided the strongest available test of the effects of changes in land cover, while accounting for other covariates (both measured [Table 2] and unmeasured).
Because we used a larger data set of watersheds for freshwater invertebrates, we employed a slightly different set of analyses for freshwater invertebrate family density and Simpson diversity. Specifically, we examined all possible pairings of the 37 watersheds using Mantel’s test. Mantel’s test is a regression in which variables are distance matrices summarizing all possible pairwise similarities among sample locations. We used it to determine whether watershed pairs that were more dissimilar in imperviousness were also more dissimilar in ecosystem properties. We converted impervious distance to non-impervious distance for these analyses in order to avoid excessive Type II error inherent to Mantel’s test when the correlations between predictor and dependent variables are expected to be negative (Legendre and Fortin 2010).

**Analyses: comparison of the strength of relationships between ecosystem properties and urbanization in freshwater and marine habitats**

To test the hypothesis that urbanization was more strongly associated with ecosystem properties within freshwater habitats than within marine habitats, we compared the strength of the impervious distance effect for biodiversity, net primary productivity, and decomposition across habitats. To ensure that effect sizes were comparable while avoiding confounding effects of different sample sizes between habitats, we standardized each habitat-specific dependent variable (by subtracting the mean and dividing by 1 standard deviation), conducted a linear regression of it against impervious distance to estimate the ‘urbanization’ coefficient, and compared this value (and its 95% CI) across habitats.
Results

Characterizing variability in urbanization, biodiversity, and ecosystem functions

The watersheds in our study captured a large range of variation in urbanization, spanning 1% to >40% imperviousness and 25% to 100% shoreline armoring. We also found considerable variation in ecosystem properties across our study sites. In marine habitats, invertebrate family density varied 6-fold (range: 3-18 families), Simpson diversity ranged almost an order of magnitude (0.07-0.79), net primary productivity varied by almost 2 orders of magnitude ($2.76 \times 10^{-4} - 1.97 \times 10^{-2}$ g day$^{-1}$), and decomposition rates varied from nil to $-0.4$ g day$^{-1}$. In freshwater habitats, invertebrate family density varied almost 5-fold (range: 6-29 families), Simpson diversity varied >3-fold (0.26-0.9), net primary productivity ranged almost a full order of magnitude ($1.02 \times 10^{-4} - 8.3 \times 10^{-4}$ g day$^{-1}$), and decomposition rates spanned a 5-fold range (-0.04 to -0.22 g day$^{-1}$). Together, the wide range of land cover and ecosystem properties we observed facilitated a strong test for associations between urbanization and ecosystem properties.

Categorical comparisons of ecosystem properties in more and less urbanized watersheds

For five of the eight ecosystem properties we tracked, more urbanized watersheds were no different than less urbanized watersheds (Fig. S1). However, marine net primary productivity (Fig. S1c) and the two measures of freshwater biodiversity (Simpson diversity and family density; Figs. S1ef) were significantly lower in more urbanized watersheds. Almost all other environmental characteristics (Table 2) did not differ between more and less urbanized watersheds (Fig. S2). (The single exception was our
detection of greater stream phosphate concentrations in less urbanized than more urbanized watersheds).

Comparisons of ecosystem properties along a continuum of urbanization

Categorical comparisons of ecosystem properties in more and less urbanized watersheds obscured the complexity of differences in urbanization among watershed pairs (Fig. 1b). In watershed pairs that were similar in imperviousness (i.e., <20% difference), more urbanized marine habitats tended to have higher family density than their less urbanized counterparts (Fig. 2). Counter-intuitively, as the impervious distance between watersheds within a pair grew large, differences in marine family density became negligible (Fig. 2; \( p = 0.01 \)). There was not an association between marine Simpson diversity distance and impervious distance (Fig. 2; \( p = 0.64 \)).

In freshwater habitats, both family density distance (Fig. 2; \( p < 0.001 \)) and Simpson diversity distance (Fig. 2; \( p < 0.001 \)) exhibited a negative relationship with impervious distance, such that more urbanized watersheds tended to have lower family density and Simpson diversity than less urbanized watersheds.

There was no association between impervious distance and either of the two ecosystem functions we tracked, net primary productivity and decomposition (Fig. 3; all \( p > 0.20 \)). In addition, the distances between other environmental characteristics (Table 2) were not significantly associated with impervious distance in either freshwater or marine habitats (Fig. S2).
Moving from land to sea: comparison of the strength of relationships between ecosystem properties and urbanization in freshwater and marine habitats

The two measures of biodiversity we tracked were negatively associated with impervious distance in marine and freshwater habitats. However, the strength of associations between family density distance and impervious distance, and that between Simpson diversity distance and impervious distance, were similar in both marine and freshwater habitats (Fig. 4). Because neither net primary productivity distance nor decomposition distance were significantly associated with impervious distance in freshwater or marine habitats (i.e., the slopes of these regression lines were not significantly different than zero; Fig. 3), we can also reject the hypothesis that urbanization was significantly more associated with freshwater ecosystem functions than marine ecosystem functions.

Discussion

As coastal cities expand, understanding their impacts on ecosystems is critically dependent on scientific knowledge about how the effects of human activities translate across terrestrial, freshwater, and marine habitats. Urbanized ecosystems generate a wide range of services on which people depend, including protection from severe weather and climate impacts, improved air and water quality, stress relief, and food production (Niemela et al. 2011). However, it is often assumed that “ecology [with]in cities” is impaired or diminished relative to without, causing urban areas to rely strongly on unpeopled ecosystems in distant, rural, and undeveloped locations (Jansson 2013). Here we found that urbanization was not associated with predictable changes in freshwater and
marine ecosystem functions (net primary productivity and decomposition) and two
different measures of biodiversity were not consistently higher in less urbanized than
more urbanized areas across freshwater and marine habitats. Where negative
relationships between our measures of biodiversity and increasing urban land cover did
exist, they were strong enough that they did not diminish between freshwater and marine
habitats. Thus, rather than suggesting that ecosystem functions are compromised,
biodiversity is uniformly lower, or marine habitats are less affected by land cover in
urban areas, these results suggest that discussion of ecology within cities and
expectations for the services they can provide require more nuanced consideration. This
conclusion adds to a growing literature which, when viewed collectively, implies that
urbanizations impacts may not be consistent, straightforward, or uniformly negative
(Table 1). Further, our findings provide at least three lessons—one hopeful, another
cautionary, and a third motivational—for coastal conservation and management.

First, our results provide some optimism in the face of the accelerating expansion
of coastal cities, as increasing urbanization was not consistently associated with
increasing impairment of two key ecosystem functions in either freshwater or marine
habitats (Fig. 3). These two functions, net primary productivity and decomposition, are
fundamental to “healthy and resilient” ecosystems (Christensen 1995, Elliott and
Quintino 2007, Samhouri et al. 2010) advocated in calls for widespread implementation
of EBM (McLeod & Leslie 2009). They underpin the production of consumer biomass
(including consumers that serve as human foods; Pauly and Christensen 1995, Brown et
al. 2004) and the efficient recycling of energy and nutrients, an archetypal regulating
service (MEA 2005). Our observations of variation in net primary productivity and
decomposition encourage increased scrutiny of the idea that urbanization undermines EBM goals focused on the maintenance of ecosystem functions. Though beyond the scope of our study, it seems likely that factors largely independent of urbanization (Fig. S2)—such as the influence of light (net primary productivity) and turbulence (decomposition)—contributed most to the wide range of spatial variability in ecosystem properties we observed. We also recognize that ecosystem properties could respond to urbanization at different spatial scales than those addressed here.

We also note that we investigated relationships between urbanization and ecosystem properties in a developed country with strong government oversight and enforcement of development and pollution regulations. A second optimistic conclusion of our work would be that careful and effective governance may reduce the potential for disparity in ecosystem properties across the urban gradient. We suspect that urbanization effects would be stronger in locales with less regulatory oversight or enforcement.

The second lesson from this research relates to oft-stated conservation and management goals that focus on broad terms such as biodiversity, ecosystem functions, and resilience (McLeod & Leslie 2009). Our work tells a cautionary tale suggesting that these terms can be unsatisfactorily coarse, making it difficult to discern which ecosystem properties are of greatest concern. Alternative indicators for a single ecosystem property can conflict, as we saw for the two measures of marine biodiversity in this study. Where changes are detected, as in this study with observations of lower macroinvertebrate family densities at more urbanized sites in both freshwater and marine habitats, clarity of purpose for choosing a particular indicator will help to inform actionable strategies for meeting conservation and management goals (Samhouri & Levin 2012).
In the Puget Sound region and beyond, it is increasingly common to observe environmental policies that call for integrated land-sea planning and ecosystem-based management that crosses traditional social-ecological boundaries (POC 2003, PSP 2008, Alvarez-Romero et al. 2011, Samhouri & Levin 2012). The third lesson from this study motivates a call for support of such initiatives, as we found that associations between ecosystem properties and urbanization did not diminish in strength between freshwater and marine habitats. This finding runs counter to others suggesting that allochthonous inputs from land are not as important as internally generated drivers in nearshore marine environments (Brett et al. 2009, Steinberg et al. 2010), and echoes more widely accepted understanding of major river influences on marine ecosystems (Diaz & Rosenberg 2008). The main difference is that in our study, we tested connections within much smaller watersheds, typically thought to be of minimal influence on coastal marine ecosystems (Smith et al. 2003, Halpern et al. 2009). Therefore, prospects for management of terrestrial, freshwater, or marine systems in isolation seem marginal, whereas integrated land-sea planning such as that spearheaded in the Puget Sound region by the Puget Sound Partnership offers greater promise.

In conclusion, rather than providing unequivocal evidence for the negative impacts of urban landscapes on biodiversity and ecosystem functions, our study supports growing evidence that a dichotomy between urbanized and non-urbanized ecological communities is less straightforward than is often assumed (Table 1). For example, the negative association between freshwater diversity and urbanization observed in this study, and established previously (Morley and Karr 2002), was striking not so much for its mean effect size (Fig. 4), but for the amount of unexplained variance around the trend
(Fig. 2). As touched on above, one interpretation of such variability is as evidence that
the long history of progressive, environmental restoration and recovery actions in the
Puget Sound region may be working, even though it is heavily developed. More broadly,
if this interpretation is correct, it lends credence to the idea that conservation attention
focused singularly on remote and relatively untouched places, and on land or at sea but
not at the interface between them, is necessary but not sufficient in the Anthropocene.

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Table 1. Examples of how urbanization, defined here as greater imperviousness and shoreline armoring, can modify environmental processes, along with expected relationships between a variety of ecosystem properties. These example studies suggest that the net effect of urbanization can lead to a broad diversity of ecosystem responses. For habitats, $F =$ freshwater, $M =$ marine. See Supporting Information for full reference information.
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<td>F</td>
<td>Algal biomass</td>
<td>None or inconsistent</td>
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<td>M</td>
<td>Gross primary productivity</td>
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<td>M</td>
<td>Standing stock biomass</td>
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Table 2. Description of data types and sampling methods. Superscripts indicate ecosystem properties likely to be associated with specific environmental characteristics. F = freshwater, M = marine, D = decomposition, I = invertebrate biodiversity, P = net primary productivity. All variables were collected from 12 study sites, except for freshwater biodiversity where we drew on 37 sites from the Puget Sound Stream benthos database. See Supporting Information for full reference information.

<table>
<thead>
<tr>
<th>Type of variable</th>
<th>Sampling Method</th>
<th>Year</th>
<th>N</th>
<th>Reference for Sampling Method</th>
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<tr>
<td>Biodiversity</td>
<td>Hess samples</td>
<td>2012-2013</td>
<td>3 site(^{-1}) year(^{-1})</td>
<td>Hauer &amp; Lamberti 2011; Wootton 2012; <a href="http://earth1.epa.gov/owow/monitoring/rbp/wp61pdf/rbp.pdf">link</a></td>
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<tr>
<td></td>
<td>Sled tows</td>
<td>2012-2014</td>
<td>3 site(^{-1}) year(^{-1})</td>
<td>Simenstad et al. 1991</td>
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<tr>
<td>Net primary productivity</td>
<td>Periphyton growth on tiles</td>
<td>2012-2013</td>
<td>10 site(^{-1}) year(^{-1})</td>
<td>Wootton 2012; Moore et al. 2007</td>
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<tr>
<td></td>
<td>Algal growth on tiles</td>
<td>2012-2013</td>
<td>10 site(^{-1}) year(^{-1})</td>
<td>Hixon &amp; Brostoff 1996</td>
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<tr>
<td>Decomposition</td>
<td>10g litter bags</td>
<td>2012-2013</td>
<td>8 site(^{-1}) year(^{-1})</td>
<td>Benfield 2006</td>
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<td></td>
<td>Zostera marina</td>
<td>2012-2013</td>
<td>8 site(^{-1}) year(^{-1})</td>
<td>Nicastro et al. 2012; Bradford et al. 2002</td>
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<tr>
<td>Environmental characteristics</td>
<td>Temperature loggers deployed in situ</td>
<td>2012-2014</td>
<td>Hourly site(^{-1}) year(^{-1})</td>
<td>Hauer &amp; Lamberti 2011</td>
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<td>Water temperature</td>
<td>Float velocity method</td>
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<td>3 times site(^{-1})</td>
<td>Rantz et al. 1992</td>
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<tr>
<td>Parameter</td>
<td>Methodology</td>
<td>Data Period</td>
<td>Frequency</td>
<td>Source</td>
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<td>-------------</td>
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<td>-----------------------------</td>
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<tr>
<td>Stream canopy cover&lt;sup&gt;FL, FP&lt;/sup&gt;</td>
<td>Densiometer</td>
<td>2012-2013</td>
<td>1 time site&lt;sup&gt;-1&lt;/sup&gt; year&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Hauer &amp; Lamberti 2011</td>
</tr>
<tr>
<td>Stream dimensions&lt;sup&gt;FD&lt;/sup&gt;</td>
<td>Depth, wetted width</td>
<td>2012-2013</td>
<td>1 time site&lt;sup&gt;-1&lt;/sup&gt; year&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Hauer &amp; Lamberti 2011</td>
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<tr>
<td>Stream sediment size&lt;sup&gt;FI&lt;/sup&gt;</td>
<td>% cobble, % gravel, % sand</td>
<td>2012</td>
<td>1 time site&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Wolman 1954</td>
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<td>Marine sediment size&lt;sup&gt;Mi&lt;/sup&gt;</td>
<td>% gravel, % sand, % fine sand</td>
<td>2013</td>
<td>1 time site&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Dethier and Schoch 2006</td>
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<td>Nutrients&lt;sup&gt;FP,MP&lt;/sup&gt;</td>
<td>NO&lt;sub&gt;3&lt;/sub&gt;&lt;sup&gt;-&lt;/sup&gt;, NH&lt;sub&gt;4&lt;/sub&gt;&lt;sup&gt;+&lt;/sup&gt;, NO&lt;sub&gt;2&lt;/sub&gt;&lt;sup&gt;-&lt;/sup&gt;, SiO&lt;sub&gt;4&lt;/sub&gt;&lt;sup&gt;2-&lt;/sup&gt;, PO&lt;sub&gt;4&lt;/sub&gt;&lt;sup&gt;3-&lt;/sup&gt; (μg/L)</td>
<td>2013</td>
<td>1 time site&lt;sup&gt;-1&lt;/sup&gt;</td>
<td><a href="http://www.ocean.washington.edu/file/Sampling+Procedures">http://www.ocean.washington.edu/file/Sampling+Procedures</a>; See Supporting Information for details</td>
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<tr>
<td>Marine salinity&lt;sup&gt;Mi&lt;/sup&gt;</td>
<td>Refractometer</td>
<td>2012-2014</td>
<td>3-5 times site&lt;sup&gt;-1&lt;/sup&gt; year&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Pilson 2012</td>
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<tr>
<td>Wave exposure&lt;sup&gt;MD, MI&lt;/sup&gt;</td>
<td>Spatial analysis of wind speed and velocity weighted fetch</td>
<td>1980-2010</td>
<td>30-year mean</td>
<td>See Supporting Information for details</td>
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</table>
Figures

Figure 1. Map of watershed locations for this study, along with a principal components analysis of watershed pairs used to define the urban gradient. Larger values of PC1 and PC2 indicate increasing urbanization.
Figure 2. Associations between impervious distance and disparity between more and less urbanized watersheds in two measures of invertebrate diversity (left, Family Density; right, Simpson Diversity) in marine (top row) and freshwater (bottom row) habitats. Solid regression lines indicate statistically significant associations, whereas the dashed lines represent zero difference in the diversity indices between more and less urbanized watersheds.
Figure 3. Associations between impervious distance and disparity between more and less urbanized watersheds in two ecosystem functions (left, Net Primary Productivity; right, Decomposition) in marine (top row) and freshwater (bottom row) habitats. No regressions were statistically significant; the dashed lines represent zero difference in the ecosystem properties between more and less urbanized watersheds.
Figure 4. Mean effect sizes (with 95% CI) for relationships between biodiversity distance (top: family density; bottom: Simpson diversity) and impervious distance in freshwater and marine habitats. Effect sizes related to two ecosystem functions (net primary productivity and decomposition) also did not differ between habitat types.
Supporting Information

Characterizing variability in urbanization and ecosystem properties: defining the urban gradient

Table S1. (a) PCA Results for urban gradient analysis.

<table>
<thead>
<tr>
<th>PC</th>
<th>Eigenvalues</th>
<th>%Variation</th>
<th>Cum.%Variation</th>
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<td>1</td>
<td>2.96</td>
<td>74.0</td>
<td>74.0</td>
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<tr>
<td>2</td>
<td>0.723</td>
<td>18.1</td>
<td>92.1</td>
</tr>
<tr>
<td>3</td>
<td>0.293</td>
<td>7.3</td>
<td>99.4</td>
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<td>4</td>
<td>2.24E-2</td>
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</table>

(b) Eigenvectors (coefficients in the linear combinations of variables making up PC's).

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<th>Variable</th>
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<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
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</thead>
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<tr>
<td>Imperviousness (%)</td>
<td>0.555</td>
<td>-0.230</td>
<td>-0.369</td>
<td>0.710</td>
</tr>
<tr>
<td>Road density</td>
<td>0.512</td>
<td>-0.142</td>
<td>0.847</td>
<td>-0.005</td>
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<tr>
<td>Armor (%)</td>
<td>0.352</td>
<td>0.934</td>
<td>-0.056</td>
<td>-0.003</td>
</tr>
<tr>
<td>Developed land (%)</td>
<td>0.554</td>
<td>-0.234</td>
<td>-0.378</td>
<td>-0.704</td>
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</tbody>
</table>

Other environmental characteristics

In addition to quantifying elements of ecosystem structure (epibenthic macroinvertebrate diversity) and function (net primary productivity and decomposition rates) in freshwater and marine habitats at each of the study watersheds, we measured several other environmental characteristics that may influence these ecosystem properties. Specifically, in both freshwater and marine habitats, we quantified water temperature hourly using in situ loggers during all sampling periods. In addition, we determined freshwater and marine water nutrient concentrations (NO3, NO2, NH4, PO4, SiOH4) by collecting samples in July 2013 (n = 3 freshwater and 3 marine samples site⁻¹).

In freshwater habitats, at the same time we were sampling ecosystem structural and functional properties, we estimated flow velocity using the float velocity method; canopy cover using a densiometer; and, stream dimensions (bankfull width, wetted width, depth) and sediment size following the protocols described by Hauer and Lamberti (2006) and others (see Table 2).

In marine habitats, we used a refractometer to estimate salinity during each site visit. We collected sediments in August 2013 to quantify grain size distributions following the methods of Dethier and Schoch (2006).

In order to characterize the relative exposure at each of our study sites, we used the Waves (v. 2012) tool (Rohweder et al. 2012) in ArcGIS to calculate a wind speed and direction weighted fetch distance for Puget Sound. We ran our model over a spatial domain spanning 47.0° to 49.5°N latitude and -122.2° to -124.6°W longitude, with a spatial grain or resolution of 50 m. The tool used two types of data: shoreline and wind. For the Canadian and the US portions of the shoreline (converted from vector to 50 m grid), we used NASA’s world surface water body data (downloaded from http://gis.ess.washington.edu/data/vector/worldshore/index.html) and USGS digital line graph (DLG), respectively. For the wind data, we used “normal” hourly wind direction and velocity for the Sea-Tac International Airport weather station (Arguez et al. 2010), based on data from 1980-2010. We used this wind station because it was central to all of
our sites and had a complete data record from 1980 – 2010. We used the SPM-Restricted option in the Waves tool to generate wind direction and speed weighted fetch distances for all of the 50 m grid cells in the study area. Finally, we overlaid the point locations for each of our marine study sites with the resulting weighted fetch distance grid and captured the relative wave exposure value for each site.

These data were used to estimate an average for each of the environmental characteristics at all of our sites during the study periods of each year.


References specific to Table 1


References specific to Table 2


Table S2. Study site characteristics.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Pair</th>
<th>Basin area (ha)</th>
<th>Imperv</th>
<th>Roads (m/ha)</th>
<th>Armor (%)</th>
<th>Devel (%)</th>
<th>PC1</th>
<th>PC2</th>
<th>Eelgrass</th>
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<tr>
<td>Clinton-Whidbey</td>
<td>P1</td>
<td>537</td>
<td>1.7</td>
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<tr>
<td>Big Gulch *</td>
<td>P1</td>
<td>671</td>
<td>33.7</td>
<td>44.6</td>
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<td>57.9</td>
<td>3.27</td>
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<td>Clearwater Casino</td>
<td>P2</td>
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<td>730</td>
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<td>13.7</td>
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<td>4.1</td>
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<td>Redondo Beach *</td>
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* more urbanized of given site pair
Table S3. Marine invertebrate taxa included in the diversity analyses.

**Marine taxa:**

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<td></td>
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<td>Batilliariidae</td>
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<td></td>
<td>Gastropoda</td>
<td>Caenogastropoda</td>
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<td></td>
<td>Calyptraeidae</td>
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<tr>
<td>Other Molluscs</td>
<td>Neoloricata Chitonida Ischnochitonidae</td>
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<tr>
<td>Neoloricata Chitonida Mopaliidae</td>
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<tr>
<td>Echinoderms</td>
<td>Asteroidea -- Unidentified asteroid</td>
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</tr>
<tr>
<td>Echinoidea Clypeasteroida Dendrasteridae</td>
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<tr>
<td>Echinoidea Echinoida Strongylocentrotidae</td>
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<tr>
<td>Holothuroidea Dendrochirotida Unidentified holothurid</td>
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<tr>
<td>Ophiuroidea Ophiurida Unidentified ophiurid</td>
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<tr>
<td>Other Taxa</td>
<td>Turbellaria -- Unidentified platyhelminthid</td>
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<tr>
<td>Anthozoa Actiniaria Actiniidae</td>
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Table S4. Freshwater invertebrate taxa and relative proportion (%) across all samples included in the diversity analyses

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Relative Proportion (%)</th>
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<tbody>
<tr>
<td>Aeshnidae (0.031)</td>
<td>Dolichopodidae (0.040)</td>
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<tr>
<td>Ameletidae (0.541)</td>
<td>Dryopidae (0.004)</td>
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<tr>
<td>Ancylidae (0.479)</td>
<td>Dytiscidae (0.616)</td>
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<td>Anisitsiellidae (0.009)</td>
<td>Elmidae (4.365)</td>
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<td>Anisogammaridae (0.093)</td>
<td>Empididae (3.328)</td>
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<tr>
<td>Apataniidae (0.301)</td>
<td>Enchytraeidae (1.604)</td>
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<tr>
<td>Arcidae (0.009)</td>
<td>Ephemerellidae (2.162)</td>
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<td>Arrenuridae (0.071)</td>
<td>Ephemeridae (0.004)</td>
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<tr>
<td>Asellidae (0.487)</td>
<td>Ephydridae (0.222)</td>
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<td>Astacidae (0.408)</td>
<td>Erpobdellidae (0.137)</td>
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<tr>
<td>Athericidae (0.053)</td>
<td>Feltriidae (0.004)</td>
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<tr>
<td>Athienemanniiidae (0.022)</td>
<td>Gammaridae (0.049)</td>
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<tr>
<td>Aturidae (0.022)</td>
<td>Gerridae (0.022)</td>
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<tr>
<td>Axonopsidae (0.004)</td>
<td>Glossiphoniidae (0.080)</td>
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<tr>
<td>Baeotidae (4.830)</td>
<td>Glossosomatidae (3.474)</td>
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<td>Blephariceridae (0.071)</td>
<td>Goeridae (0.031)</td>
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<td>Brachycentridae (1.427)</td>
<td>Gomphidae (0.053)</td>
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<tr>
<td>Caenidae (0.035)</td>
<td>Gyrinidae (0.004)</td>
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<td>Calamoceratidae (0.031)</td>
<td>Haliplidae (0.093)</td>
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<td>Capniidae (0.425)</td>
<td>Haplotaxidae (0.018)</td>
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<tr>
<td>Carabidae (0.009)</td>
<td>Helicopsychidae (0.018)</td>
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<td>Ceratopogonidae (2.477)</td>
<td>Helophoridae (0.004)</td>
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<td>Chaoboridae (0.004)</td>
<td>Heptageniidae (3.438)</td>
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<td>Chironomidae (5.078)</td>
<td>Hirudinidae (0.004)</td>
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<td>Coenagrionidae (0.097)</td>
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<td>Corixidae (0.075)</td>
<td>Hydrobiidae (0.261)</td>
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<tr>
<td>Corophiidae (0.049)</td>
<td>Hydrodromidae (0.004)</td>
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<tr>
<td>Family</td>
<td>Percentage</td>
</tr>
<tr>
<td>-----------------</td>
<td>------------</td>
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<td>Crambidae</td>
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<td>Hydrophilidae</td>
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<td>Hydropsychidae</td>
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<td>Pisidiidae</td>
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<td>Dixidae</td>
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<td>Hygrobatidae</td>
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<tr>
<td>Planorbidida</td>
<td>0.793</td>
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</table>
Figure S1. Results from paired t tests examining differences between more and less urban sites within a pair in each of 8 ecosystem properties. Figures represent 95% confidence intervals, such that negative values with CIs that do not overlap zero suggest a greater value of the ecosystem property in less urban sites (marine primary productivity, stream family density, stream Simpson’s diversity) and vice versa (none).

For more than half of the ecosystem properties we tracked, more urbanized watersheds were no different than less urbanized watersheds (only 3 of 8 paired t-tests were significant). In marine habitats invertebrate family density tended to be higher, and Simpson diversity tended to be lower, in more urbanized than less urbanized watersheds, though neither of these differences was significant. In contrast, marine net primary productivity was significantly lower in more urbanized than less urbanized watersheds, but there was no significant difference in marine decomposition between more and less urbanized watersheds. In freshwater habitats, more urbanized watersheds were characterized by significantly lower invertebrate family density and Simpson diversity than less urbanized watersheds. Neither of the ecosystem functions we measured in freshwater habitats differed between more and less urbanized watersheds.
Figure S2. Environmental characteristics likely to be associated with biodiversity (F: summer stream water temperature, stream flow, stream dimensions; M: summer marine water temperature, exposure), net primary productivity (F: summer stream water temperature, stream canopy cover, stream nutrient concentrations; M: summer marine water temperature, marine nutrient concentrations), and decomposition (F: fall stream water temperature, stream flow, stream dimensions; M: fall marine water temperature, exposure) did not differ significantly between more and less urban watershed pairs or change significantly with increasing impervious distance. The only exception was for stream PO4 concentrations, which were significantly higher in less urban than more urban watersheds. (a) Summer stream water temperature, (b) Fall stream water temperature, (c) Stream flow, (d) Stream dimensions, (e) Stream canopy cover, (f) Stream nutrient concentrations, (g) Summer marine water temperature, (h) Marine exposure, (i) Marine nutrient concentrations.

(a) Summer stream water temperature
(b) Fall stream water temperature

Mean delta MEAN.s.temp.NovDec.2013

95% CI of more – less urban

Delta MEAN.s.temp.NovDec.2013 (more – less urban)

Delta Impervious (more – less urban)
(c) Stream flow

Mean delta flow m.s JulAug.2012

Mean delta flow m.s JulAug.2013

Delta impervious (more - less urban)
(d) Stream dimensions

- Mean delta avg.Sept.wetted.width.m
- 95% CI of more − less urban

- Delta avg.Sept.wetted.width.m (more − less urban)
- Delta Impervious (more − less urban)
(e) Stream canopy cover

![Graph showing mean canopy cover differences between more and less urban areas]
(f) Stream nutrient concentrations

- **Mean delta Stream.PO4**
- **Mean delta Stream.SiOH4**
- **Mean delta Stream.NO3**
- **Mean delta Stream.NO2**
- **Mean delta Stream.NH4**
(g) Summer marine water temperature

Mean delta MEAN.m.temp.2012

Mean delta MEAN.m.temp.2013

Mean delta MEAN.m.temp.Jul.2014

Mean delta MEAN.m.temp.JunJul.2013
(h) Marine exposure

![Graph showing marine exposure changes](image)

- Mean delta Exposure m.1980-2010
- 95% CI of more - less urban

![Graph showing delta exposure changes](image)

- Delta Exposure m.1980-2010 (more - less urban)
- Delta Impervious (more - less urban)
(i) Marine nutrient concentrations

- Marine.PO4

- Marine.SiOH4

- Marine.NO3

- Marine.NO2

- Marine.NH4