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PRIMARY RESEARCH PAPER

Identifying natural catchment landscape influences on tropical stream organisms: classifying stream reaches of the Hawaiian Islands

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Abstract Stream classifications can be used to understand patterns within and across river networks and are most informative when they offer insight into patterns in stream habitat or biology. We developed a classification of Hawaiian stream reaches based on influences of natural landscape features on distributions of stream organisms to understand patterns in ecological potential across five Hawaiian Islands. Our objectives were to (1) identify natural landscape variables strongly associated with species distributions and likely to affect stream habitat; and (2) classify Hawaiian stream reaches based on relationships between landscape variables and distributions of native stream taxa. We used canonical correspondence analysis to identify natural landscape variables associated with distributions of nine native stream taxa. To classify reaches, we then used a conditional inference tree that identified significant influences of natural landscape variables on taxa distributions and showed that elevation, channel slope, hydrologic soil grouping, and rainfall were all important predictors of species distributions. Results were used to develop reach classes that describe differences in stream habitat. Our research adds to current understanding of landscape controls on the biota of tropical island streams and provides a tool for decision makers tasked with developing conservation and adaptation strategies.

Keywords Classification · Hawaii · Ecology · Hierarchical

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Introduction

Streams are composed of diverse habitats that vary throughout networks and influence distributions of aquatic organisms (Robinson et al., 2002; Ward et al., 2002). Variation in habitat throughout networks is in part the result of variation in geology, topography, and climate operating across landscapes drained by streams (e.g., Hynes, 1975; Frissell et al., 1986), and such hierarchical influences of landscape features on stream organisms through habitat are well described (e.g., Wiens, 2002; Allan, 2004). Studies that fully account for mechanistic influences of landscape features on stream habitats and organisms are beneficial for developing conservation strategies because results can suggest prescriptive steps for management (e.g., Fausch et al., 2002; Wang et al., 2006; Newton et al., 2008), such as modifying landscape features or, more commonly, their effects on habitat to improve conditions for stream organisms (e.g., Wang et al., 2003; Kaufmann & Hughes, 2006; Zorn & Wiley, 2006; Infante & Allan, 2010). In addition, understanding relationships between climate-influenced habitat conditions and stream organisms can improve our ability to anticipate effects of climate change and develop adaptive management strategies. However, such studies rely on co-occurring stream habitat and biological datasets, which are not always available and are rarely inclusive of all streams across a study region. This is problematic for managers charged with conserving stream habitat, who often require an understanding of variation in habitat and biology over large spatial extents (i.e., states, ecoregions) in their entirety to develop and prioritize conservation or management action across many streams.

Stream classifications are analytical tools that can aid in clarifying complex patterns in habitat throughout networks and over large regions, and can provide insights for managers into the diversity of habitat that may be available (Melles et al., 2012). Early stream classifications described changes in stream size based on drainage patterns through upstream networks, and their approaches remain generalizable across systems (e.g., Horton, 1945; Strahler, 1952). Other broadly applicable but more complex classifications show differences in streams based on physical characteristics of their channels (e.g., slope and sinuosity) and catchments (e.g., Rosgen, 1994; Montgomery & Buffington, 1997; Brierley & Fryirs, 2000). Recently, increases in availability of landscape-scale datasets as well as improved geospatial data processing capabilities have supported stream classifications derived by grouping stream units with similar physical characteristics over large study regions. For example, Snelder & Biggs (2002) classified all streams in New Zealand based on differences in climate, geology, topography, and land cover variables summarized within stream catchments and found to influence stream habitat. Across Luxembourg, Ferreol et al. (2005) clustered streams using elevation, catchment geology, and stream size to create broad stream types, which were further described using site-specific physical and chemical characteristics. While effective in summarizing differences in streams over large regions, classifications based only on physical characteristics of stream catchments and channels may not be fully effective at accounting for ecological differences that could occur across classes, potentially limiting their effectiveness in efforts to conserve aquatic organisms.

When possible, using distributions or abundances of stream organisms to identify important catchment or channel characteristics and/or breaks in those characteristics can provide greater ecological insight for classifying streams than using physical characteristics alone. One approach for incorporating biology is to treat information on species or species assemblages as independent classifying factors in addition to physical variables. Seelbach et al. (2006) developed ecologically homogenous stream units across the Lower Peninsula of Michigan, U.S. based on the presence of fish species with varied thermal preferences along with catchment surficial geology, land cover, and relative amounts of groundwater delivery to streams. In the U.S. Pacific Northwest, Higgins et al. (2005) grouped adjacent catchments into larger regions termed ecological drainage units based on similarities in landscape characteristics and historical fish distributions within catchments. While using biological data as an independent variable is one approach for classification, an alternative approach is to develop classes based on identified relationships between landscape and biological variables on a subset of rivers where both types of data are available. Such an approach can approximate mechanistic influences of physical landscape characteristics on biology. Additionally, while biological data are often only available for a subset of streams within a large region, landscape data describing channels and catchments are often continuous, allowing for extrapolation of classification results to all streams, including those lacking biological data. Brenden et al. (2008) implemented such an approach in the Lower Peninsula of Michigan, U.S. by first identifying influences of stream size, channel gradient, and modeled water temperature on stream fish assemblages from several hundred sites. They then classified streams across the study region using the identified landscape variable values that generated the most homogenous groupings of stream fish assemblages (Brenden et al., 2008). This approach is based on the hierarchical understanding that physical landscape characteristics influence fish through controls on habitat and allows for a representation of a stream's ecological potential, which we define as the ability to support a species given the hydrologic, chemical, and physical characteristics of its habitat.

On tropical islands formed by volcanic processes, stream assemblages often include endemic species requiring consistent hydrological connections between freshwater and marine habitats to complete life histories (Fitzsimons et al., 2002; Kikkert et al., 2009; Jenkins et al., 2010; Bauer, 2013). Differing species' habitat requirements and migratory abilities combined with variation in natural landscape characteristics create complexity in assemblage patterns throughout river networks. In many of these regions, species are highly threatened by habitat degradation resulting from urban and agricultural land use as well as habitat loss due to stream flow diversions (Brasher, 2003; Smith et al., 2003; Jenkins et al., 2010). Climate change will also impact these species through alterations to flow regimes, as the tropics are anticipated to experience regionally specific changes in total rainfall and increases in the number and intensity of extreme events (IPCC, 2013). Greater understanding of the spatial distribution of habitat through the development of stream classifications can be an important step to aid in habitat protection and contribute to the persistence of native species on volcanic tropical islands.

The goal of this study is to classify Hawaiian stream reaches based on influences of natural landscape features on distributions of native stream fish, decapods, and snails. Our first objective is to identify a set of natural landscape variables that are most strongly associated with distributions of native stream taxa. Our second objective is to classify Hawaiian stream reaches based on identified relationships between the influential natural landscape variables and taxa distributions. Resulting classes of stream reaches will highlight the ecological potential of streams across Hawaii and will identify rare and common habitats associated with different taxa, while also providing insight into landscape influences on stream organisms in volcanic tropical island streams.

Materials and methods

Study region

Perennial streams are found throughout the five largest Hawaiian Islands: Hawaii, Molokai, Maui, Oahu, and Kauai (Fig. 1), and islands increase in age from east to west. Volcanic activity ceased on Kauai approximately 6 million years ago, while southern Hawaii Island experiences episodic lava flows. Hydraulic conductivity of the islands' geology varies due to differences in age and direction of lava flows (e.g., vertical dikes resulting from lava flows can impound groundwater), leading to substantial differences in groundwater contributions to stream baseflow, especially during periods of low rainfall (Izuka et al., 2015). Due to prevailing trade winds, leeward sides of each island are generally drier than windward sides, and the majority of perennial streams occur on windward sides of islands. Together, these landscape factors contribute to diverse stream habitat conditions across islands, including stream flow regimes that range from intermittent flows in high rainfall areas to perennial flows in dry areas due to substantial groundwater inputs. Native Hawaiian stream organisms, excluding benthic insects, include five species of fish (four in the family Gobiidae and one in Eleotridae), two decapods (*Atyoida bisulcata* Randall, 1840 and *Macrobrachium grandimanus* Randall, 1840), and two neritid snails (*Neritina granosa* Sowerby, 1825 and *Neritina vespertina* Sowerby, 1849; Kinzie, 1990). These species are amphidromous: they hatch in streams, spend a short time (weeks–months) developing in the marine environment, and then migrate upstream to mature and reproduce (McDowall, 1988). Coastal species, most notably flagtails (*Kuhlia* sp.) and striped mullet (*Mugil cephalus* Linnaeus, 1758), also move between streams and estuarine habitats (Nishimoto et al., 2007; McRae et al., 2011).

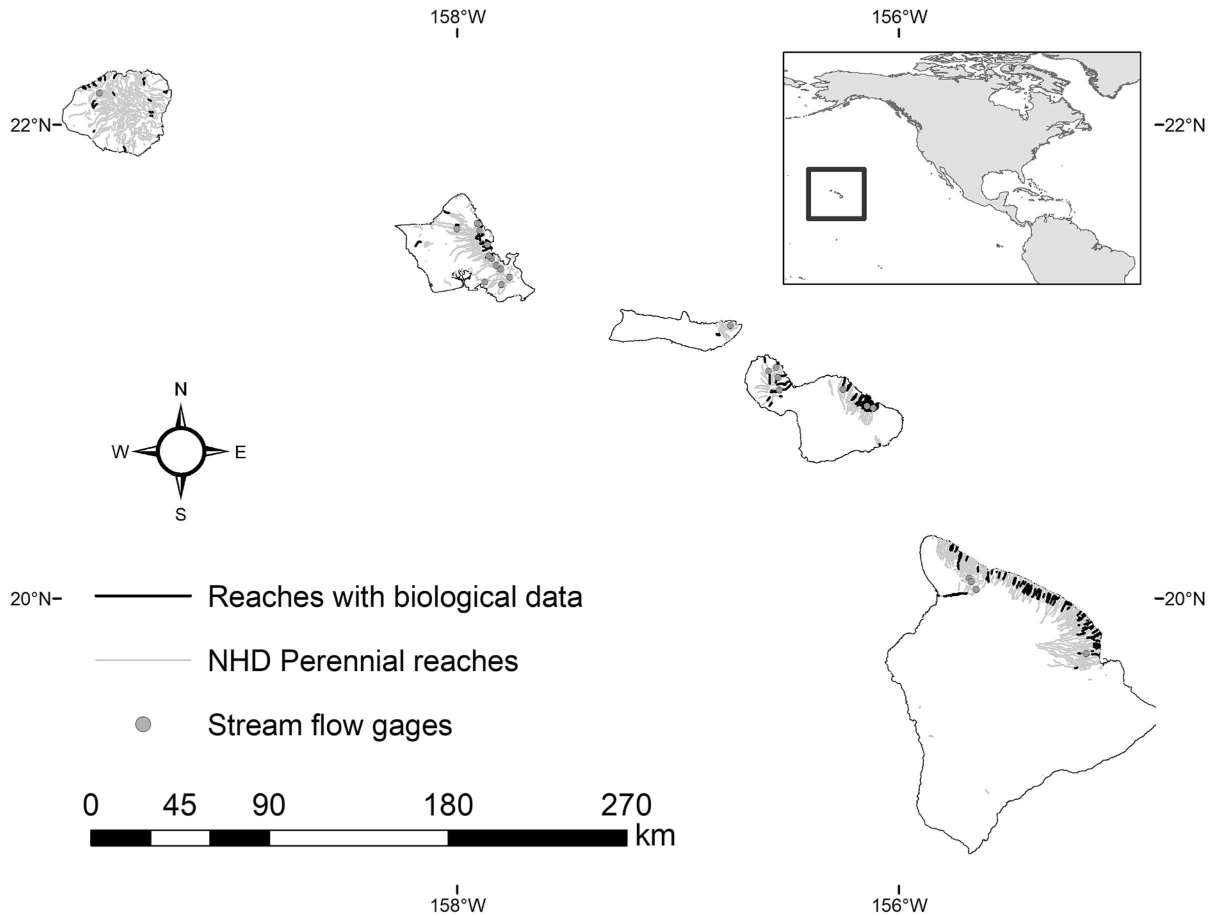

Fig. 1 Study area and stream reaches with biological data

Spatial framework and natural and biological datasets

Spatial units and framework

We modified the 1:24,000 National Hydrography Dataset (NHD; Simley & Carswell Jr., 2009; http://nhd.usgs.gov/) for the five main Hawaiian Islands to create a consistently defined and ecologically meaningful set of spatial units (termed stream reaches; Wang et al., 2011) to use as the basis for our spatial framework. The NHD characterizes natural and artificial fluvial pathways across the Hawaiian landscape by a set of discrete stream lines. We first excluded stream lines representing artificial channels, including ditches and canals, because we chose to classify only natural fluvial pathways. We next removed inter-confluence stream breaks within the NHD (e.g., line breaks at USGS Topographic Quadrangle Maps boundaries) following Wieferich et al. (2015) to group adjacent stream lines occurring between stream confluences. This was done to generate a more ecologically meaningful representation of streams devoid of artificially defined (non-hydrologic) stream breaks. Because waterfalls were underrepresented within the NHD dataset, we used the Hawaii Division of Aquatic Resources waterfall layer (http://hawaii.gov/dbedt/gis/waterfalls.htm) to create stream line breaks at waterfall locations. In addition, we divided stream lines where they intersected ecological zone boundaries associated with changes in elevation known to influence stream organisms throughout the Hawaiian Islands (Parham & Lapp, 2006). This step was taken to ensure that analyses could most effectively discriminate between groups of streams based on differences in their ecological potential. Our alterations to the NHD result in an independent stream layer with 4732 individual perennial stream reaches across the study area.

We defined three area-based spatial units as part of the spatial framework for our study region: local catchments, upstream catchments, and downstream main channel catchments specific to each stream reach. We delineated local catchments, or the area of landscape draining directly to the stream reach (Wang et al., 2011), using the modified hydrography layer and a 10-m digital elevation model (DEM) from the National Elevation Dataset (NED; http://ned.usgs.gov/) within the ArcMap extension ArcHydro 9.0. We generated upstream catchments, or the entire upstream area draining to a given stream reach, by converting the local catchment grid to a polygon layer, and then accumulated all upstream local catchments for each stream reach to generate a nested polygon layer that included an individual polygon for each reach's upstream catchment. We used the ArcGIS extension Network Analyst (http://www.esri.com/software/arcgis/extensions/networkanalyst) to establish upstream connectivity and to aggregate landscape data within the upstream catchment. We also used Network Analyst to establish downstream connectivity and develop the downstream main channel catchment, which represents the area of the landscape draining directly to the portion of the stream that connects a given reach to the marine environment.

Natural landscape variables

We considered 11 natural landscape variables for analysis assumed to be influential to stream habitat and distributions of stream organisms based on expert opinion and relationships established in previous Hawaiian stream research (Table 1, Kido, 2008; Parham et al., 2009). Categories of natural landscape variables included stream size and channel slope, influences on migration, soil characteristics, and rainfall. More information on specific variables and their attribution to our spatial framework are described below.

Stream size was reflected by upstream catchment area, while stream reach slope was calculated based on change in elevation between the upstream end of a stream reach and its downstream end divided by reach length. We also estimated downstream main channel slope using elevation change between the midpoint of a reach and the pour point of the downstream main channel into the marine environment. Variables describing influences on migration included minimum elevation, distance inland, and maximum waterfall height. We determined minimum elevation of each stream reach using the modified hydrography dataset and the 10 m DEM to estimate elevation at the end point of a given reach. We also measured distance from the midpoint of stream reaches to the marine environment along the channel, called distance inland. We estimated maximum waterfall height encountered in the downstream main channel using values from the World Waterfall Database (www.worldwaterfalldatabase.com). In instances where waterfalls were identified along the stream channel and heights were not available in the World Waterfall Database, we used Google Earth and the 10-m DEM to approximate waterfall height. Soil characteristics were represented using the Soil Survey Geographic Database (SSURGO; USDA, 1995) and included variables describing soil infiltration and erodibility. SSURGO hydrologic soil groupings (Groups A, B, C, D) represent relative differences in runoff potential; Group A soils have the lowest runoff potential, while Group D soils have the highest runoff potential. High potential runoff in Group D soils can be due to low soil infiltration rates, water tables that are permanently high, or a shallow soil layer over impervious materials. In Hawaii, Group D soils representing areas with short distances to impervious materials may overlap with high-elevation groundwater resources impounded by dikes (i.e., rock outcrops; Lau & Mink, 2006). We assigned numerical codes to the hydrologic groupings as 4 (A), 3 (B), 2 (C), and 1 (D) and summarized the area-weighted average within local catchments to generate a continuous variable, hydrologic soil grouping. We also identified the local catchment with the lowest hydrologic soil grouping in the upstream network and assigned this value to a given reach (termed upstream minimum hydrologic soil grouping). We summarized average SSURGO soil erodibility, classed as highly erodible (3), potentially highly erodible (2), and not highly erodible (1), for both local and upstream catchments. Mean annual rainfall in the upstream catchment was summarized from average monthly rainfall values for the period 1992–2007 (Frazier et al., 2016) and was selected from an initial set of 70 rainfall variables for inclusion in analysis through a multi-step variable reduction process (additional details in Online Resource 1).

Table 1 Landscape variables considered for use in the Hawaiian stream classification

Category	Code	Variable description	Units	Spatial scales
Stream size and channel slope	AREAKM	Upstream catchment area	km^2	U*
	SLOPE	Reach slope	%	L*
	MC_SL	Main channel slope	%	D*
Influences on migration	MIN_ELE	Reach elevation	m	L*
	DIST_IN	Reach distance inland	km	L
	DROP_WF	Maximum waterfall height	m	D*
Soil characteristics	HY	Hydrologic soil grouping	–	L
	MIN_HY	Minimum hydrologic soil grouping	–	U*
	EROD	Soil erodibility	–	U,L
Rainfall	MAR	Mean annual rainfall	mm/year	U*

Variables were summarized at three spatial scales: local (L), upstream (U), and downstream main channel (D) catchments. Soil erodibility was summarized at multiple spatial scales, resulting in 11 natural landscape variables. Asterisks (*) indicate the 7 variables that were used in the conditional inference tree to generate stream classes

Biological data

Presence–absence data used in this analysis were collected by the Hawaii Division of Aquatic Resources, capturing distributions of organisms occurring in stream reaches any time from 1992 to 2010 (i.e., current distributions). Because we were attempting to characterize ecological potential of stream reaches, or the ability of a stream to support a given taxa, we used all sampling results to establish presence or absence to avoid potentially excluding taxa that could be supported by the reach. We also based this decision on the understanding that when sampling methods help identify when species are absent from a sample, that information should be used to give improved insights into species prevalence analyses and modeling (Elith et al., 2011). A total of 403 perennial stream reaches were attributed with biological data (see Tingley III, 2017 for additional details). The final dataset used to classify stream reaches characterizes current distributions of eight amphidromous native stream taxa (five fish species, two freshwater decapod species, and a neritid gastropod species) and one grouping of two kuhliid estuarine fish species that periodically access streams from the nearshore marine environment (Table 2).

Identification of influential natural landscape variables

We used a forward selection canonical correspondence analysis (CCA) within the program CANOCO

Table 2 Stream taxa used in the ecological classification of Hawaiian streams

Taxa	Common name	Taxa group	Taxa code	Percent reaches with taxa (%)	Present in sampled perennial reaches				
					Hawaii	Maui	Molokai	Oahu	Kauai
Atyoida bisulcata	’opae kala’ole	Decapod	1	38.0	Y	Y	Y	Y	Y
Lentipes concolor	o’ opu alamo’o	Fish	2	35.5	Y	Y	Y	Y	Y
Sicyopterus stimpsoni	o’ opu nopili	Fish	3	35.7	Y	Y	Y	Y	Y
Awaous stamineus	o’ opu nakea	Fish	4	46.4	Y	Y	Y	Y	Y
Neritina granosa	hihiwai	Snail	5	24.3	Y	Y	Y	Y	Y
Eleotris sandwicensis	o’ opu ‘akupa	Fish	6	12.2	Y	Y	N	Y	Y
Stenogobius hawaiiensis	o ’opu nahina	Fish	7	6.0	Y	Y	N	Y	Y
Macrobrachium grandimanus	opae oeha’a	Decapod	8	5.2	Y	Y	N	Y	Y
Kuhlia sp.	āholehole	Fish	9	13.2	Y	Y	N	Y	Y

to identify those natural landscape factors (log($x + 1$) transformed, following Wang et al., 2001) most strongly associated with species distributions. Forward selection CCA is an ordination technique used in ecological studies to identify factors explaining variation in a set of dependent variables (e.g., Wang et al., 2003; Esselman & Allan, 2010). Using CCA, we identified those variables that were at least weakly associated ($P < 0.15$) with the biological dataset and excluded those with limited association from the classification of stream reaches.

Ecological classification of stream reaches

Conditional inference tree analysis

We generated a conditional inference (CI) tree to classify stream reaches into groups based on similarities in relationships between natural landscape variables and native stream taxa distributions. CI tree analysis is a recursive partitioning technique that maximizes differences among groups based on differences in a set of predictor variables. We used CI tree analysis because it allows for generating groupings based on relationships between multiple predictor variables and multiple binary responses (Hothorn et al., 2006). We also chose this technique because it addresses overfitting of the tree and the bias towards predictor variables with many possible breaks by incorporating a two-step splitting and stopping procedure that tests for statistical significance at each split (Hothorn et al., 2006).

We used the function "ctree" within the R package "party" to generate the initial CI tree describing relationships between the natural catchment landscape variables and taxa distributions within study reaches. An individual CI tree was generated using data from 323 sites, while the remaining 80 sites were withheld for validation. The alpha value was set to 0.05 with a Bonferroni adjustment to account for multiple tests, and the minimum bucket size (the number of reaches that must be present in a terminal node for a split to occur) was set to 20, equal to ~ 5% of the original dataset.

Following the creation of the initial tree, we identified alternative splits at each node to determine whether additional significant relationships between natural landscape variables and taxa distributions were present. Examining alternative splits in recursive partitioning analysis can suggest the influence of alternative predictor variables that may also have strong relationships with the response dataset at a given node, yielding more simplistic trees or greater ecological understanding (De'ath & Fabricius, 2000). To validate relationships between natural landscape variables and the biological dataset identified by the CI tree, we calculated Area under the curve (AUC) estimates for each reach class based on assemblage results within each class. Area under the curve is often used to examine the predictive capabilities of conditional inference trees and other recursive partitioning techniques (e.g., Zipkin et al., 2012; Blank & Blaustein, 2014).

Finalizing reach classes and examining taxa associations

We used the output of the CI tree as the basis for developing the ecological stream classification of the 4732 perennial stream reaches in Hawaii. In addition to the CI tree results, two additional reach classes, headwater reaches and reaches with terminal falls, were created to account for established ecological relationships between natural landscape variables and distributions of native stream taxa (see Online Resource 2). To fully depict habitat patterns across islands, we also applied classification results to reaches not classed as perennial in the NHD but that provide consistent hydrologic connectivity between perennial headwaters and the marine environment (e.g., mainstem of the Hanalei River on Kauai) due to their importance for amphidromous species. Stream taxa were considered associated with a particular reach class when percent occurrence was greater in the reach class than across all sampled reaches (Liu et al., 2005).

Results

Study site description

Natural landscape features varied across the study region (Table 3). Mean upstream catchment area was 15.9 km^2, and only 10% of stream reaches had catchments larger than 31.4 km^2. Ninety percent of all stream reaches had local slopes greater than 1.8%, indicating that most reaches have high gradient. While the average distance inland for perennial reaches was 8.8 km, mean minimum reach elevation was 352.9 m,

Table 3 Descriptive statistics for all natural landscape variables summarized for perennial stream catchments across the study region (*n* = 4732) and for those with biological samples (*n* = 403)

Category	Mean	Median	10th percentile	90th percentile
All perennial stream reaches				
Upstream catchment area (km^2)	15.86	2.39	0.20	31.44
Local reach slope (%)	19.01	9.80	1.80	48.50
Downstream main channel slope (%)	9.09	4.40	0.80	15.60
Minimum reach elevation (m)	352.91	236.50	16.00	773.00
Distance inland (km)	8.82	6.51	0.16	21.47
Upstream soil erodibility (1–3)	2.37	2.38	1.97	2.99
Local soil erodibility (1–3)	2.40	2.49	1.65	3.00
Local hydrologic soil grouping (1–4)	1.80	2.00	1.00	2.80
Upstream minimum hydrologic soil grouping (1–4)	1.50	1.10	1.00	2.30
Upstream mean annual rainfall (mm/year)	3254.00	3106.00	1563.80	5171.20
Perennial stream reaches with biological samples				
Upstream catchment area (km^2)	18.74	8.00	3.00	43.00
Local reach slope (%)	11.05	7.70	3.70	22.16
Downstream main channel slope (%)	9.81	6.10	2.60	17.36
Minimum reach elevation (m)	154.48	95.00	21.00	370.00
Distance inland (km)	3.80	2.54	0.72	8.83
Upstream soil erodibility (1–3)	2.41	2.33	2.11	2.94
Local soil erodibility (1–3)	2.40	2.47	2.03	3.00
Local hydrologic soil grouping (1–4)	1.92	2.00	1.23	2.72
Upstream minimum hydrologic soil grouping (1–4)	1.46	1.20	1.00	2.00
Upstream mean annual rainfall (mm/year)	3420.23	3419.00	1798.60	5104.00

which suggests substantial elevation gains over short distances from the nearshore environment. Mean annual rainfall varied substantially across perennial reaches, with a 10th percentile value of 1564 mm/year and a 90th percentile value of 5171 mm/year. Comparison of natural landscape features for all reaches versus those with biological samples were similar. Catchment areas were similarly sized (18.7 km^2 for reaches with samples vs. 15.9 km^2 for all reaches), as was downstream main channel slope (9.8% in reaches with samples vs. 9.1% in all reaches). Average upstream mean annual rainfall was similar among reaches with biological samples and the entire reach dataset (3420 and 3254 mm/year, respectively). Factors that were lower in sampled reaches versus the larger set of perennial reaches included distance inland (3.8 vs. 8.8 km, respectively), minimum stream elevation (154.5 vs. 352.9 m, respectively), as well as measures of channel slope. These differences reflect the fact that biological samples were not typically collected in difficult-to-access high-elevation reaches.

The goby *Awaous stamineus* (Eydoux & Souleyet, 1850) was the most common taxa found in Hawaiian streams, occurring in nearly half of all sampled stream reaches (46.4%; Table 2). Two gobies (*Lentipes concolor* Gill, 1860 and *Sicyopterus stimpsoni* Gill, 1860) and one species of atyid (*A. bisulcata*) were found in just over one-third of all sampled stream reaches (35.5, 35.7, and 38.0%, respectively). The prawn *M. grandimanus* and goby *Stenogobius hawaiiensis* (Watson, 1991) were least common and were found in only 5.2 and 6.0% of sampled stream reaches, respectively. The amphidromous neritid snail, *N. granosa*, was found in 24.3% of sampled reaches. All taxa were observed in streams on Maui, Hawaii, Oahu, and Kauai, while only five of the nine were sampled in streams classified as perennial within the NHD stream layer on the island of Molokai (Table 2).

Influential natural landscape variables

Overall, 26% of the total variance in the biological dataset was explained by landscape variables included in the forward selection CCA. Of the explained variance, 94% was attributed to seven landscape variables: upstream catchment area, local reach slope, downstream main channel slope, reach elevation, maximum waterfall height in the downstream main channel, upstream minimum hydrological soil grouping, and mean annual rainfall (Table 1). Local and upstream soil erodibility, local hydrologic soil grouping, and reach distance inland had limited association with the species distribution datasets and were therefore not used in the stream reach classification.

Ecological classification of stream reaches

Conditional inference tree

The CI tree resulted in nine classes of stream reaches (A–I) defined by relationships between natural landscape variables and the biological dataset (Fig. 2; Table 4). Minimum elevation had the strongest association with taxa distributions at three out of eight nodes (values at which the CI tree splits sample reaches into two subsequent groups of reaches) within the CI tree, generating splits within the dataset at 22, 76, and 233 m (nodes I, II, and VII, respectively; Fig. 2). Downstream main channel slope had the strongest relationship with the biological dataset in low-elevation reaches (22 m $> X \leq$ 76 m). Stream reaches above 76 m in elevation and with catchments

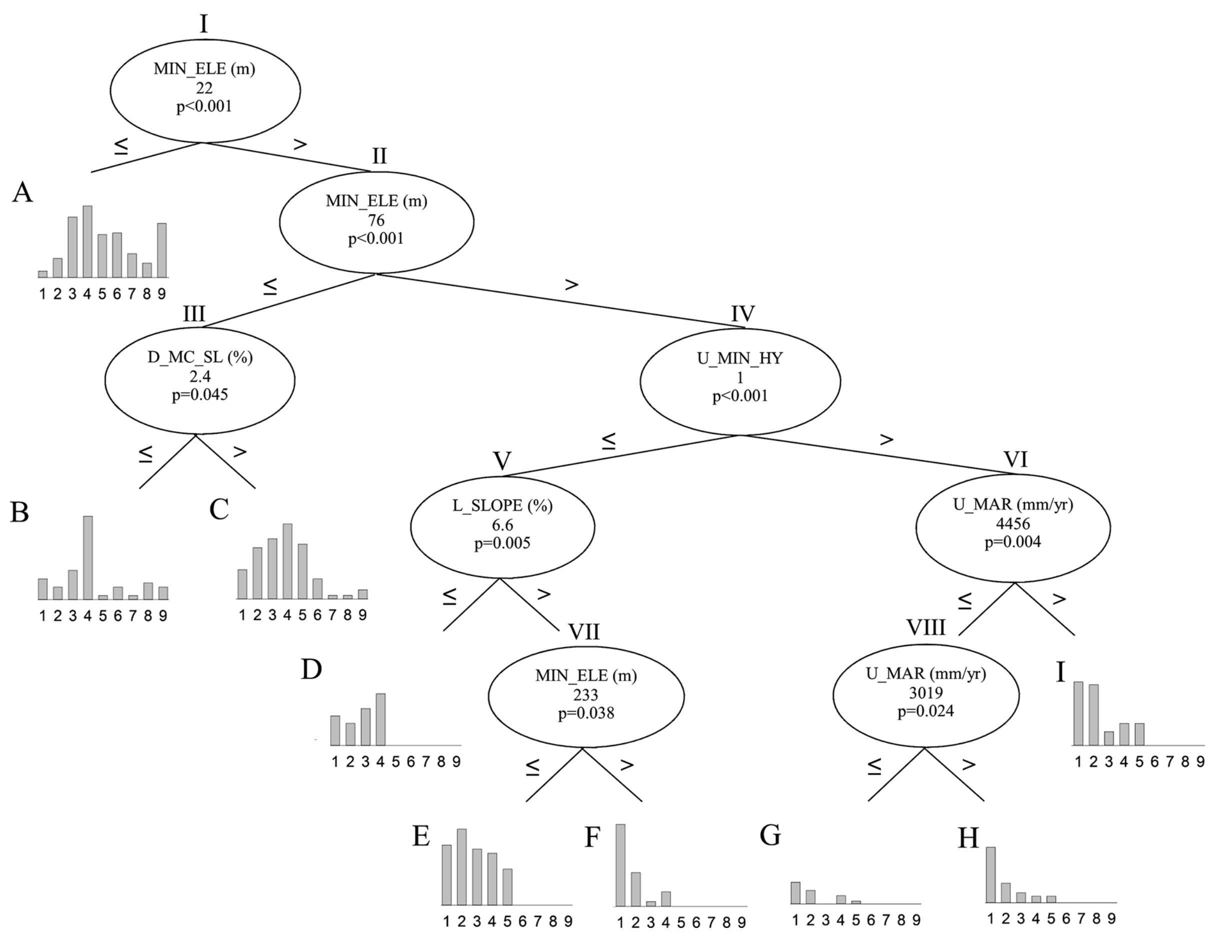

Fig. 2 Conditional inference tree and resulting characteristics of reach classes (A–I). The relative species occurrence is represented within each histogram by its taxa value (1–9). Nodes (I–VIII) indicate landscape variables associated with significant splits in taxa distributions

Table 4 Descriptions, area under the curve (AUC) values for validation datasets, and associated taxa for each stream reach class

Reach class	Description	Validation AUC	Associated taxa
A	Coastal	0.71	*S. stimpsoni*, *A. stamineus*, *N. granosa*, *E. sandwicensis*, *S. hawaiiensis*, *M. grandimanus*, *Kuhlia* sp.
B[a]	Low-gradient downstream channel at low elevation	N/A	*A. stamineus*, *M. grandimanus, E. sandwicensis, Kuhlia* sp.
C	High-gradient downstream channel at low elevation	0.78	*L. concolor, S. stimpsoni*, *A. stamineus*, *N. granosa*, *E. sandwicensis*
D	Low gradient, moderate to high elevation, high runoff potential/water table	0.86	*A. stamineus, S. stimpsoni*
E	High gradient, moderate elevation, high runoff potential/water table	0.91	*A. bisulcata, L. concolor, S. stimpsoni*, *A. stamineus*, *N. granosa*
F	High gradient, high elevation, high runoff potential/water table	0.88	*A. bisulcata*
G	Moderate to high elevation, low rainfall	0.71	
H	Moderate to high elevation, moderate rainfall	0.87	*A. bisulcata*
I	Moderate to high elevation, high rainfall	0.95	*A. bisulcata, L. concolor*
J	Terminal falls at low elevation	N/A	*A. bisulcata, L. concolor*
K	Headwater streams	N/A	

[a]AUC was not calculated for the validation dataset of reach class B due to low sample size (number of reaches = 1)

composed of soils with relatively lower runoff potential or greater distance to the underlying water table (i.e., excluding soil grouping D) were grouped into reach classes delineated by differences in upstream mean annual rainfall. In a single instance, an alternative variable (upstream mean annual rainfall; Node VIII) was chosen to replace the original split variable (local slope) to generate a more simplistic and ecologically meaningful tree. Overall, AUC values (ranging from 0.71 to 0.95) indicate that the analysis was effective at delineating reaches into classes based on relationships between taxa distributions and landscape variables (Table 4). Area under the curve values at or below 0.5 would suggest the analysis was ineffective in delineating reach classes, poor if less than 0.69, fair to good if between 0.70 and 0.89, and excellent if greater than 0.90 (Swets, 1988; Blank & Blaustein, 2014).

Reach classes across the islands

The number of taxa associated with each reach class varied from 7 (reach class A) to 0 (G; Table 4). In general, number of taxa associated with a given reach class declined with increasing elevation and with lower mean annual rainfall. When the specific break values associated with individual landscape characteristics are used to classify all perennial stream reaches, they show a diversity of stream habitats exists across the Hawaiian Islands (Fig. 3). On the island of Oahu, low-gradient, low-elevation stream habitats are common, and 15.6% of total perennial stream length is class A (Table 5). The high-gradient, low-elevation reach class C is more prominent on the islands of Hawaii, Maui, and Molokai, while the lower gradient reach class B is more common at low elevations on Kauai and Oahu. On the island of Maui, the majority of streams present on the eastern half of the island above 76 m in elevation are in classes distinguished by differences in mean annual rainfall (H and I), while the western half is dominated by reach classes D, E, and F. Headwater reaches (class K) and reaches at low to moderate elevations with low rainfall (class G) were most common across the entire study area (19.1 and 18.1% of perennial stream length, respectively). Kauai is dominated by reach class F in catchments that extend to high elevations near the center of the island. Reach class K is found across all islands and makes up the highest proportion of perennial stream reaches on Hawaii Island (25.8% of total stream

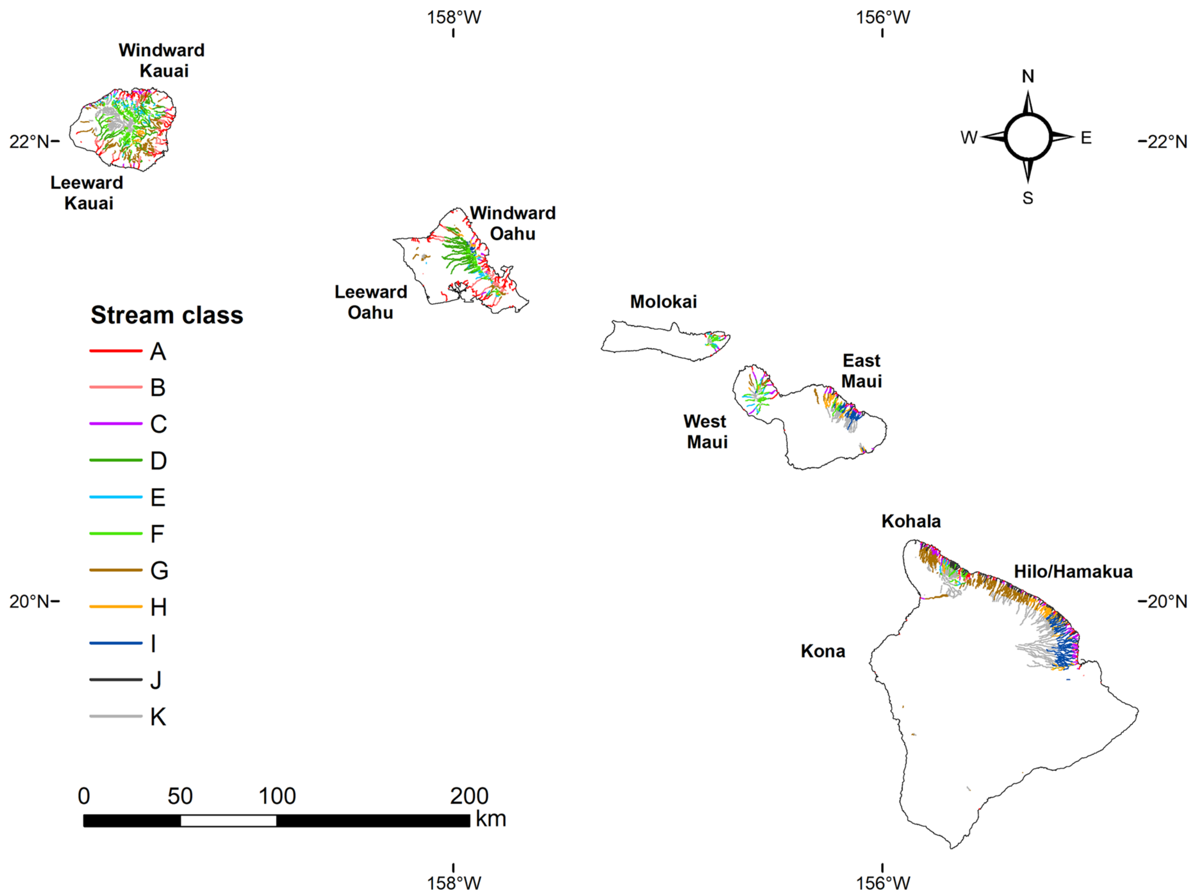

Fig. 3 Final classification of Hawaiian stream reaches

Table 5 Percent of the total perennial stream length across and within individual islands of each reach class

Reach class	All islands	Hawaii	Maui	Molokai	Oahu	Kauai
A	6.1	2.5	3.5	6.1	15.6	6.5
B	4.9	0.9	0.2	1.6	12.2	8.1
C	4.5	6.3	8.5	8.4	1.5	2.0
D	12.9	0.9	2.6	4.8	40.4	17.4
E	4.0	1.2	4.7	15.4	5.0	6.1
F	11.5	4.3	14.8	46.6	9.5	18.3
G	18.1	24.8	8.3	2.6	8.8	19.7
H	6.3	8.5	13.9	1.3	2.9	2.8
I	9.2	17.5	16.7	0.0	2.6	0.0
J	3.2	7.2	2.7	0.4	0.0	0.4
K	19.1	25.8	24.3	12.6	1.5	18.8

length). Together, these results provide a holistic view of habitat diversity across Hawaiian Islands at a fine spatial scale.

Discussion

In this study, we selected a set of natural landscape variables strongly associated with native stream taxa distributions, and then developed a reach classification based on specific relationships between these landscape variables and distributions of individuals. Given that our classification approach stems from the idea that landscape characteristics influence biology, the variables identified by the CCA as having associations with taxa distributions are likely reflective of mechanistic influences of landscape on stream taxa via controls on habitat. Several of the natural landscape variables found to have strong relationships with distributions of native stream taxa through the CCA, such as rainfall, channel slope, elevation, and upstream catchment area, are known to influence the distribution on stream organisms in many other systems globally, while others may be more regionally important. Relationships between landscape variables and species in the classification are in some cases suggestive of potential differences in habitat across reaches. For instance, differences in mean annual rainfall among streams with similar physical characteristics (i.e., geology, elevation) may reflect differences in steam flow magnitude. Also, because of the landscape variable split values identified within the CI tree, all stream reaches within the study region can be assigned to classes, broadly characterizing ecological potential of Hawaiian stream reaches. The classification can be used to consider the location of common and rare habitat types, which has relevance for development of adaptation strategies to various stressors (e.g., climate change, increased spread of invasive species). In addition, as many volcanic tropical islands share common genera (Smith et al., 2003), the relationships between landscape variables and stream species generated to develop the classification may also be valuable in informing classifications on other volcanic tropical islands where species-specific data are lacking.

Landscape variables strongly associated with stream taxa distributions

The results of the CCA highlight similarities and differences between natural landscape influences on stream habitats in Hawaii and those in other regions. Rainfall (e.g., DeRolph et al., 2015), hydrologic soil groupings indicative of differences in soil infiltration or groundwater input (e.g., Stauffer et al., 2000; Brewer et al., 2007), channel slope (e.g., Maret et al., 1997; Walters et al., 2003), and upstream catchment area (e.g., Wang et al., 2003) all have been shown to have strong relationships with stream habitats and species distributions in stream systems across the world. Elevation is associated with differences in species assemblage in Hawaii and other tropical systems (e.g., Polhemus et al., 1992; Parham & Lapp, 2006; Parham et al., 2009) and is also a variable commonly used in stream classifications in other regions (Melles et al., 2014). In contrast, other natural landscape variables are more commonly associated with differences in taxa distributions in Hawaii and similar systems. For example, maximum waterfall height is associated with differences in species composition in tropical island streams and has been used to depict spatial patterns in species assemblages in Hawaii (Parham & Lapp, 2006). In streams of New Zealand where amphidromous species are common, differences in fish and macroinvertebrate distributions were linked to differences in average downstream main channel slope (Leathwick et al., 2011). Together, these results suggest that commonalities in the hierarchical effects of landscape on biology exist across many stream systems, but regionally specific studies can provide further insight into understanding of a stream's ability to support aquatic biota.

Ecological classification of stream reaches

Influences of landscape variables on stream taxa distributions

The results of the CI tree are useful in considering the influence of landscape characteristics on stream taxa distributions. Among the natural landscape variables examined in this study, minimum reach elevation had the strongest influence on taxa distributions across all sampled reaches. In addition, the individual break values associated with two of the three elevation splits (22 and 233 m) are similar to those used previously with waterfall height to broadly classify Hawaiian streams into biological zones (20 and 200 m), showing agreement in our quantitative approach with an existing ecoregional classification in Hawaii (Parham & Lapp, 2006). The importance of elevation in defining stream reach classes results from differing abilities of individual taxa to ascend steep reaches and instream barriers (Polhemus et al., 1992; Nishimoto & Fitzsimons, 2006) and is reflected by specific taxa associated with each reach class. For instance, the association of *A. bisulcata* and in some instances *L. concolor* with high-elevation reach classes is likely due to their abilities to traverse most natural barriers in Hawaii. Similarly, the association of nearshore (*Kuhlia* sp.) and non-climbing taxa (*Eleotris sandwicensis* Valliant and Sauvage, 1875, *M. grandimanus*, *S. hawaiiensis*) with low-elevation classes coincides with the current understanding that with increasing elevation the location of a single significant migratory barrier along the stream network prevents further upstream migration.

We also found that reach classes with higher channel slopes were associated with different taxa assemblages than reach classes with lower slopes. Channel slope is known to be a primary factor in determining stream power, or a stream's ability to move material, and lower gradient reaches may therefore have more fine material than higher gradient reaches (Knighton, 1998). In our study, the association of certain stream taxa with higher sloped stream classes at low elevations may be related to an increase in foraging opportunities. Limited fine sediment in reaches with higher slopes may benefit herbivorous stream taxa (*N. granosa*, *S. stimpsoni*) that feed by scraping diatoms and algae from surface of cobble and boulder (Fitzsimons et al., 2007). In addition, reaches with higher slopes may also have increased stream velocity, resulting in increased delivery of fine particulate organic matter (FPOM) to filter feeders (*A. bisulcata;* Couret Jr., 1976). Preferential habitat selection may also be reflected in taxa associations in low-gradient reach classes. For instance, despite moderate climbing abilities, *A. stamineus* is associated with low-elevation and lower gradient reach classes. This may be due to a habitat preference for deep, slow pools where *A. stamineus* forages for macroinvertebrates by burrowing within fine sediments, a unique feeding strategy not exhibited by other Hawaiian gobies (Kinzie & Ford, 1982; Kinzie, 1988).

Our results also indicate that the amount of rainfall that occurs within a catchment influences habitat of Hawaiian stream reaches. This is not surprising, as differences in mean annual rainfall likely reflect broad differences in total available habitat and the likelihood of low flow/drying events. The CI tree results also indicate that effects of rainfall on taxa distributions are most important in systems that are less likely to be influenced by high-elevation groundwater resources (as indicated by values of upstream minimum hydrologic soil grouping greater than 1). This result has particular relevance for understanding differences in the sensitivity of Hawaiian stream reaches to climate change and also highlights the benefits of implementing approaches that allow for the consideration of how landscape variables predict ecological potential.

Inventory of classes across the Hawaiian Islands

Differences in the prevalence and distribution of reach classes within and across islands emphasize the importance of considering reach-to-reach variation in ecological potential when assessing freshwater resources in Hawaii. A higher percentage of lower elevation, lower gradient reach classes on Oahu and Kauai indicates that the majority of habitat associated with non-climbing and nearshore taxa occur on these islands. This gradient in the increased availability of low-elevation habitat from younger to older islands mirrors a pattern observed in a classification of Hawaiian watersheds (Parham, 2002; Parham et al., 2008). The most common reach classes at moderate to high elevations from east to west along the island chain are also indicative of physical landscape characteristics that differ with island age. For instance, perennial streams on older islands with greater channel incision are more likely to be influenced by high-elevation dike-impounded groundwater that contributes to baseflow (Craig, 2003; Lau & Mink, 2006; Izuka et al., 2015). While we were able to partially capture this relationship using the break in upstream minimum hydrologic soil grouping identified in the CI tree, the development of an island-wide groundwater spatial dataset would increase the ability to classify stream reaches based on unique groundwater inputs (i.e., perched groundwater or unique geologic characteristics; Izuka et al., 2015). In addition, the misidentification of streams as intermittent or null in the NHD dataset may result in several rivers that have perennial flows, most notably on the northern draining slopes of Molokai, being excluded from our analysis and subsequently the classification. Additional efforts to improve the categorization of stream flow within the NHD would be a useful step in furthering stream research and promoting effective conservation.

Utility for conservation

In Hawaii, endemic decapods, fish, and snails are threatened by increasing human landscape disturbance, invasive species, and climate change (Brasher, 2003; Smith et al., 2003; Walter et al., 2012). The stream reach classification developed in this study can be used to account for natural variation in stream reaches to increase understanding of ecological patterns and responses to threats, which can in turn aid in management for conservation or adaptation. For example, the results of the stream classification allow for the visualization of differences in habitat across the islands, which can be used in spatial prioritization analyses that identify areas of conservation importance based on unique habitats and associated biotic assemblages. Finer-resolution biological data (i.e., abundance data, disease prevalence, growth rates of individuals in different habitats) can be examined within or across classes to assess how disturbances may affect stream populations. The classification can also be paired with human disturbance datasets and habitat condition measures to assess which habitats and taxa are at greatest risk from human disturbance. The classification also has the potential to be valuable in assessing Hawaiian stream vulnerability to climate change by utilizing downscaled projected climate change data to assess how or if streams may experience shifts in reach class with changing climate. For example, a stream reach with rainfall as an important determinant of class may experience declines in suitable habitat if mean annual rainfall declines, therefore indicating these streams may be more vulnerable to climate change than streams in classes that may have substantial groundwater contributions to baseflow.

Conclusion

The results of our study suggest that natural landscape features of Hawaiian catchments and stream channels are influential to the distribution of stream taxa, and that these relationships can be used to develop a study area-wide classification of stream reaches. A strength of this study is that while we relied on biological data to inform the generation of stream classes, even unsampled reaches were classified, allowing for a spatial representation of stream resources beneficial to conservation planning. We chose to conduct our study in Hawaii to demonstrate the value of such an approach in regions like tropical islands of the Pacific, which support many stream organisms that are threatened by disturbance from anthropogenic land use and potential changes in climate. However, development of stream classifications using such an approach is beneficial for informed conservation decision making in any system where variation in and interactions among natural landscape features have inherently complex relationships with stream habitat and biota.

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