CONSERVING STREAMS WITH CHANGING CLIMATE: A MULTI-SCALED RESEARCH FRAMEWORK TO CONSIDER CURRENT AND FUTURE CONDITION OF HAWAIIAN STREAM HABITATS

By

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ABSTRACT

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Human land use in stream catchments and direct alterations to stream channels have degraded stream habitats across the world, which in turn has resulted in declines in biodiversity. In addition, climate change has and will continue to alter stream habitat and lead to additional changes in species distributions and characteristics of existing populations, which in some cases, may lead to species extinction. Given the current degraded condition of stream habitats and potential effects of climate change, effective conservation of stream species requires that decision-makers anticipate climate change and incorporate knowledge on its effects into conservation strategies (i.e., proactive conservation). Proactive conservation therefore requires that current influences of climate on streams and the organisms they support are understood. However, observed effects of climate on organisms depend on the scale over which they are examined. Studies at multiple spatial extents can increase our understanding of climate change effects on streams in different ways and can provide effective insights when they are complementary. The goal of my dissertation is to implement a research framework that increases understanding of climate influences on streams over multiple scales in support of proactive conservation. I applied this framework across the five largest Hawaiian Islands, where little research has been conducted on effects of climate on stream organisms. In these chapters, I examined the influence of climate on native stream organisms over two spatial scales, the entirety of study area, which has a wide range in rainfall and other natural landscape features, and within a region of Hawaii Island with little variability in most landscape features but a

gradient in mean annual rainfall. I then used my results to inform a spatial prioritization approach that identified areas of high conservation value given potential changes in rainfall. I found that across the entire study area, influences of climate and other natural landscape features on species distributions could be used to characterize differences in stream habitats across Hawaii, while over smaller spatial extents, influences of rainfall on native stream species population characteristics (i.e., individual size, disease occurrence) were observed indirectly through influences of flow magnitude, variability, and the occurrence of low flows. The results of the spatial prioritization of stream habitats indicated that many areas capable of supporting unique stream habitats and taxa assemblages will continue to do so as rainfall magnitude changes through the 21st century, but some streams will experience annual or seasonal drying that may result in a shift in their ability to support taxa. My study generated useful information on potential effects of climate on species in Hawaii and demonstrated the value of considering changes in population characteristics of stream organisms to understand underlying mechanisms that may drive species loss with climate change. In addition, the multi-scale framework implemented in my study can be applied in other understudied regions that require information on influences of climate on stream ecosystems to inform proactive conservation decisionmaking.

Copyright by RALPH WILLIAM TINGLEY III 2017 To Mom, Dad, Bea, Laura, Rob, George, and Samwise

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PREFACE

The major research chapters in this dissertation have been prepared and formatted for publication. Therefore, there is some repetition in concept, study site descriptions and methods among chapters.

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INTRODUCTION

Current rates of species extinction are estimated to be several orders of magnitude greater than historical baselines (Pimm et al., 2013), and approximately one in three freshwater vertebrate species are threatened with extinction across the world (Collen et al., 2014). In streams, habitat degradation resulting from indirect effects of anthropogenic land use and channel and flow alterations has contributed substantially to declines in abundance and species extinctions (Allan et al., 2004; Dudgeon et al., 2006; Helfman, 2007). Further degradation of freshwater habitats is likely to occur as anthropogenic disturbance to the landscape continues to increase over the 21st century (Martinuzzi et al., 2014). The identification of areas that support stream species of conservation interest is therefore a priority of management agencies and conservation partnerships alike (e.g., USFWS, 2006; American Rivers, 2013). However, future effects of changing climate on stream habitats and the species they support may confound conservation actions if only current condition is taken into account.

Over the last half century, effects of increasing air temperature and changes in precipitation resulting from climate change have been observed in streams in multiple regions. Hari et al. (2006) linked increases in air temperature to reductions in available habitat and increases in disease occurrence for brown trout, *Salmo trutta*, in streams of Switzerland. In the Pacific Northwest, U.S.A., Ward et al. (2015) associated declines in the natural reproduction of Chinook salmon, *Oncorhynchus tshawytscha*, with increases in winter stream flow variability likely resulting from a greater number of winter rainfall events. In addition, changes in the distribution of stream fishes resulting from changes in climate have been documented across the globe (as reviewed by Comte et al., 2013). As temperatures continue to rise and regional precipitation changes, gains or losses in species distributions (e.g., Mohseni et al. 2003; Comte et

al., 2013; Domisch et al., 2013), changes in population characteristics (i.e., abundance, growth, occurrence of disease; e.g., Pease and Paukert, 2014), and higher rates of extinction of stream species (e.g., Xenopoulos et al., 2005; Tedesco et al., 2013) are all projected to occur.

The current state of stream systems and potential effects of climate change suggest that to effectively conserve stream species and their habitats we must incorporate knowledge on anticipated changes in air temperature and precipitation into conservation decision-making (Palmer et al., 2009; Zeigler et al., 2012). Therefore, understanding habitat factors most important to stream organisms as well as their response to changes in these conditions (i.e., water temperature, stream flow) are necessary to develop effective conservation strategies. These responses include both changes in species distributions as well as underlying changes to characteristics of populations, such as disease prevalence and fecundity and growth of individuals, which may ultimately threaten population persistence. However, understanding organism response to climate change can be difficult, given that influences of precipitation and rainfall are context-dependent, and biotic response to stream habitat will vary depending on the spatial scale over which it is examined (Heino et al., 2007; Gornish & Tylianakis, 2013).

Across large spatial extents, regional differences in climate and interactions of climate with geology, topography and other natural landscape features within stream catchments control stream habitat and in turn influence distributions of stream organisms (e.g., Hynes, 1975; Frissell, 1986; Allan, 2004). By first understanding influences of landscape factors on species distributions over large spatial extents, we can more effectively examine the response of population characteristics to climate-mediated habitat changes within smaller regions with less variability in landscape features. These responses can then provide richer insight into underlying mechanisms that may eventually lead to population loss (Whitney et al., 2016) while also

providing information on the value of a given stream system for species conservation.

Therefore, studies that increase our understanding of effects of climate change on stream species over several spatial scales can complement one another to improve proactive conservation decision making.

Tropical island streams often support endemic species of fish and shrimp that require hydrologic connections to marine habitats to complete their amphidromous life history (Fitzsimons, 2002; Kikkert et al., 2009; Jenkins et al., 2010; Bauer, 2013). Variation in habitat requirements and migratory abilities results in complex patterns of species distributions within stream catchments and across islands. Tropical island streams and the species they support have been historically understudied, but the need for research grows as climate change progresses and anthropogenic disturbance, largely from land use and channel alteration, increases (Smith et al., 2003). Because many tropical-island 1st and 2nd order streams are dependent on persistent rainfall for perennial stream flows due to low groundwater input (Craig, 2003) and because they provide important habitat for many endemic species, alterations to precipitation magnitude or frequency resulting from climate change may have severe effects on stream organisms (Leong et al., 2004). Given the severity of current and future threats, greater understanding of differences in stream habitats within and among island systems and their relationships to natural landscape features, including rainfall, can be useful in understanding differences in habitat sensitivity to change and ultimately to prioritizing conservation actions.

The goal of my dissertation was implement a research framework that increases understanding of climate influences on streams over multiple scales in support of proactive conservation. I focus my research on the sub-tropical Hawaiian Islands where effects of climate on Hawaiian stream systems have historically received little attention, yet declines in annual

rainfall over the last century have been associated with declines in baseflow (Bassiouni & Oki, 2013; Frazier & Giambelluca, 2016) and regional declines in rainfall are projected to continue (Timm et al., 2015). I begin by identifying influences of the natural landscape on distributions of stream organisms across the five largest Hawaiian Islands with perennial streams, which I then use as the basis for development of an ecological classification of streams at the reach scale across the islands. Then, over a set of reaches with similar landscape characteristics, I assess influences of rainfall on the stream flow regime and in turn, influences of the stream flow regime on population characteristics of an endemic atyid shrimp, *Atyoida bisulcata*. Finally, using the ecological classification of reaches and projected climate data, I identify areas across the five islands that are projected to retain high conservation value under both current and future conditions. My research will increase our understanding of climate change effects on tropical island streams by examining biological response to climate over multiple spatial scales, providing information that can help inform and implement proactive conservation of the unique stream organisms of the Hawaiian Islands.

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CHAPTER 1

INFLUENCES OF NATURAL LANDSCAPE FACTORS ON TROPICAL STREAM ORGANISMS: AN ECOLOGICAL CLASSIFICATION OF HAWAIIAN ISLAND STREAMS

Abstract

Natural landscape features influence stream biology through controls on stream habitat. While this hierarchical relationship is widely acknowledged as important to the understanding of stream systems and has been supported by several studies at small spatial extents, regional differences in natural landscape controls on habitat and complexity due to variation in natural landscape features over large spatial extents are less well understood. Ecological stream classifications are useful tools that can describe some of this complexity over large study areas and are especially valuable when habitat can be inferred from influences of natural landscape data on stream organisms. In this study, we develop a classification of Hawaiian stream reaches based on influences of natural landscape features on stream habitat and biota. Our objectives include 1) identifying a parsimonious set of natural landscape variables that are anticipated to influence stream habitat and are associated with distributions of stream taxa; and 2) classifying Hawaiian stream reaches by identifying influences of specific natural landscape variables on distributions of stream taxa. An initial data reduction process that included use of a forward selection canonical correspondence analysis (CCA) resulted in a set of 7 natural landscape variables that have strong associations with distributions of stream taxa in Hawaii, some of which are commonly identified to influence habitat in many systems and some that are regionally specific. A conditional inference tree was then used to identify significant influences of these 7 natural landscape variables on taxa distributions. Results indicate that stream taxa distributions in Hawaii are well described by differences in elevation, channel slope, groundwater delivery and rainfall. These results were used to develop 12 reach classes that, when extrapolated using

available spatial datasets across the five largest Hawaiian Islands, describe differences in stream habitat and associated taxa. This research adds to our current understanding of landscape controls on the aquatic biota of tropical island streams and provides a useful tool for decision makers who require system-wide understanding of stream habitats at fine spatial scales.

Introduction

Streams are comprised of diverse habitats that vary throughout networks and influence local biodiversity (Robinson et al., 2002; Ward et al., 2002). Patterns in habitat are in part the result of natural landscape features, such as geology, topography, and climate, operating across landscapes drained by streams (e.g., Hynes, 1975; Frissell et al., 1986). Principles of landscape ecology support this understanding of interrelationships, including the emphasis on habitat heterogeneity being driven in part by landscape factors as well as hierarchical influences of landscape factors on stream organisms through effects on habitat (Wiens, 2002; Allan, 2004). Accounting for such relationships is now considered essential when conducting stream studies (Fausch et al., 2002), but influences of natural landscape features on stream biota are often complex and difficult to characterize over large spatial extents. Further, most studies that have documented influences of landscape features on biota via habitat are limited in spatial extent, focusing on a few catchments (e.g., Roth et al., 1996; Infante & Allan, 2010) or relatively small regions (e.g., Richards et al., 1997; Wang et al., 2003; Infante et al., 2006; Dala-Corte et al., 2016; Paller et al., 2016). Additional research is therefore required to identify regional differences in landscape effects on stream ecology over large spatial extents.

Stream classifications are analytical tools that can aid in clarifying complex patterns in stream characteristics, including landscape influences on habitat, across large regions (Melles et al., 2012). A broad goal of many stream classifications is to describe and categorize physical

characteristics of stream habitats or their catchments. Early stream classifications were developed to describe changes in stream size based on drainage patterns throughout upstream networks (e.g., Horton et al., 1945; Strahler, 1952). Other more complex classifications have summarized differences in segments of streams based on characteristics including sinuosity, geology, and channel slope (e.g., Rosgen, 1994; Montgomery & Buffington, 1997; Brierley & Fryris, 2000).

Recent increases in availability of landscape-scale datasets as well as improved geospatial data processing capabilities have supported classifications of stream systems derived from physical characteristics of stream channels and catchments across large spatial extents. Snelder & Biggs (2002) applied the River Environment Classification (REC) to all streams of New Zealand, classifying stream segments based on differences in climate, geology, topography, and land cover known to have important influences on stream habitat. Parham et al. (2002) used similarities in size and shape of stream catchments, network stream channel slope, and extent of bay development at catchment pour points to classify Hawaiian streams and estimate habitat availability for stream fishes. The above classifications are based on physical characteristics of stream channels or catchments and effectively summarize potential differences in stream habitats over large regions, but they lack explicit links between landscape factors, habitat features they are attempting to characterize, and stream organisms.

Using biological data for stream classifications can yield greater ecological insights by linking physical characteristics of the channel and catchment to biological patterns across a study area. In the Pacific Northwest region of the U.S, Higgins et al. (2005) grouped adjacent catchments into large spatial units (Ecological Drainage Units) based on similarities in natural landscape features and historical fish distributions within catchments. Seelbach et al. (2006)

identified segments of Michigan streams with similar types of catchment surficial geology and land cover, amounts of groundwater delivery to segments, and presence of fish species, resulting in identification of ecologically homogenous stream units across the Lower Peninsula. The aforementioned studies developed classifications by assessing patterns in natural landscape features and patterns in biology independently, then combining this information to group units into ecologically similar classes.

An alternative to this approach involves using statistical analyses to group a subset of stream units into homogenous groupings based on influences of natural landscape variables on species then using identified relationships to classify all streams within the study area that may lack species data. Brenden et al. (2008) implemented such an approach in the Lower Peninsula of Michigan by identifying influences of stream size, channel gradient and modeled water temperature on stream fishes, then extrapolating this information to reaches lacking fish data to develop an ecological stream classification (Brenden et al., 2008). This type of classification approach allows for greater understanding of the natural ability of a stream to support aquatic biota, or its ecological potential. In addition, it allows for identification of influences of natural landscape features on stream biota via habitat independent of a stream unit's position within the study area, thereby identifying influences that may have been masked if streams were first clustered into groups (Leathwick et al. 2011). Stream classifications that describe ecological potential using identified influences of natural landscape features on stream organisms are grounded in current ecological theory, can provide insight into the relative importance of individual natural landscape features in shaping local biodiversity, and are particularly useful for classifying streams across large areas of interest where biological data are not available within all stream units.

Tropical island streams are historically understudied systems that support unique biological assemblages. Assemblages often include endemic species that require surface hydrological connections between freshwater and marine habitats to complete amphidromous life histories (Fitzsimons, 2002; Kikkert et al., 2009; Jenkins et al., 2010; Bauer, 2013). Differing habitat requirements and migratory abilities for each species combined with variation in natural landscape features of catchments and stream channels control differences in distributions of species throughout individual river networks. In many tropical island systems, species are threatened by habitat degradation from agricultural and urban land use, which results in pollution, alterations to stream temperature regimes, and sedimentation, as well as habitat loss due to extensive diversions or alterations of stream flow (Brasher et al., 2003; Smith et al., 2003; Jenkins et al., 2010). In addition, current climate change projections for the tropics indicate regionally specific shifts in rainfall, with some regions experiencing wetter conditions and others experiencing reductions in rainfall (IPCC, 2013). Therefore, many tropical island streams may be subject to reductions in rainfall, in some cases resulting in reductions in stream flow. Given the severity of current and future threats, greater understanding of differences in stream habitats across island systems and their relationships to natural landscape features, including rainfall, can be useful in prioritizing conservation action and understanding differences in habitat sensitivity to change.

The goal of this study is to develop a classification of Hawaiian stream reaches based on influences of natural landscape features on stream organisms. To meet this goal, our first objective is to identify a parsimonious set of natural landscape variables that are anticipated to influence stream habitat, are available across the entire study area, and that are strongly associated with distributions of stream organisms. Our second objective is to classify Hawaiian

stream reaches by identifying influences of specific natural landscape variables on distributions of stream taxa, and then extrapolate results across the study area using available spatial datasets. The resulting stream classes will highlight the ecological potential of stream reaches across Hawaii while allowing for the identification of rare and common habitats associated with different taxa, which in turn can help prioritize conservation actions.

Methods

Study region

This study evaluated perennial streams of the five largest Hawaiian Islands: Hawaii, Molokai, Maui, Oahu, and Kauai (Figure 1.1). The islands increase in age from east to west. Volcanic activity ceased on Kauai approximately 6 million years ago, while portions of Hawaii Island currently experience new lava flows. Hydraulic conductivity of underlying geology varies due to differences in age and direction of lava flows (e.g., vertical dikes resulting from flows can impound groundwater), leading to substantial differences in groundwater contributions to stream baseflow, especially during periods of low rainfall (Lau & Mink, 2006, Izuka et al., 2015). Due to prevailing trade winds, leeward sides of each island are generally drier than windward sides (Giambelluca et al., 2011), 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 flow regimes ranging from intermittent streams that only flow during major precipitation events to perennial streams that have continuous flow throughout the year due to groundwater inputs.

Spatial framework and natural and biological datasets

Spatial units and framework

As the basis for the spatial framework for this study, we modified the 1:24,000 National Hydrography Dataset (NHD 2008; http://nhd.usgs.gov/) to create a consistently-defined and ecologically-meaningful set of spatial units for analysis. We began by evaluating all arcs (i.e., spatial representations of surface water channels) in the NHD for the five main Hawaiian Islands, and we excluded those that were classified as ditches or canals; only arcs classified as perennial or intermittent were used for development of the spatial framework. Second, we modified breaks in some stream arcs in two ways. In many cases, arcs in the NHD represent ecologically-defined sections of streams extending between stream origins and confluences; confluences and confluences; or confluences and lotic water bodies, river mouths, or in some cases, waterfalls. However, arcs in the NHD could also be defined by non-ecological criteria, including stream arc intersections with boundaries of USGS Topographic Quadrangle Maps. To eliminate this artifact of the NHD, we identified arcs defined by topographic line intersections with streams and then grouped sets of adjacent arcs that would otherwise comprise a single, ecologically-defined unit (following Wieferich et al., 2015). In addition, waterfalls were underrepresented within the NHD dataset and were supplemented using the Hawaii Division of Aquatic Resources waterfall layer (http://hawaii.gov/dbedt/gis/waterfalls.htm) to create additional arc breaks. The third step in modifying the NHD was to divide arcs 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 stream arcs based on differences in their ecological potential. Through these modifications, we developed the Hawaii Fish Habitat

Partnership (HFHP) stream layer (http://www.fishhabitat.org/). We refer to individual arcs within this modified hydrography layer as stream reaches (following Wang et al., 2011).

We created catchment boundaries to encompass landscapes that drain directly to stream reaches in the HFHP stream layer, referred to as local catchments (Wang et al., 2011). We generated local catchments using the ArcMap extension ArcHydro 9.0. We reconditioned a 10 m DEM from the National Elevation Dataset (NED; http://ned.usgs.gov/) to the HFHP stream layer while filling sinks across the landscape, then generated a flow direction grid that was subsequently used to create local catchments for each reach within the spatial framework.

We generated two additional spatial units as part of the spatial framework for our study region. First, we defined upstream catchments, or the entire upstream area draining to a given stream reach, by converting the local catchment grid to a polygon layer, then generating a nested polygon layer that included an individual polygon for each reach's upstream catchment. Next, we used the ArcGIS extension Network Analyst

(http://www.esri.com/software/arcgis/extensions/networkanalyst) to generate a matrix that connected single stream reaches with all upstream reaches to establish directionality and to aggregate landscape data within the upstream catchment. Finally, we used Network Analyst to establish downstream connectivity and develop the downstream main channel catchment, which represents the portion of the stream connecting a given reach to the marine environment. *Natural landscape variables*

To characterize important natural landscape feature influences on distributions of stream organisms in Hawaiian streams, we began our analysis with 82 variables summarized in multiple spatial scales (Table 1.1). All landscape datasets used to generate variables were publically available or created for this study. Variables were considered for analysis based on expert

opinion and relationships established in previous research (Kido, 2008; Parham et al., 2009). Categories of natural landscape variables included stream size and channel slope, influences on migration, soil characteristics, and rainfall.

Stream size and channel slope

We first calculated catchment area for each upstream catchment, a representation of stream size. Next, we calculated stream reach slope from the change in elevation between the uppermost point of a stream reach and its terminal end divided by total reach length. Finally, we calculated downstream main channel slope using the elevation change between the terminal point of a reach and the point of the downstream main channel where the stream enters the marine environment.

Influences on migration

We determined the minimum elevation of each stream reach using the HFHP stream layer and the 10 m DEM to estimate elevation at the terminal point of a given reach. We also measured the distance inland from the terminal point of stream reaches to the marine environment along the channel. We estimated maximum waterfall height using information available in the World Waterfall Database (www.worldwaterfalldatabase.com), available elevation data, and Google Earth. For each stream reach, we then calculated maximum waterfall height in the downstream main channel.

Soil characteristics

Characteristics of soil and geology across the study region were represented using attribute data within the Soil Survey Geographic Database (SSURGO; USDA, 1995). SSURGO hydrologic soil groupings are classed into four types (Groups A, B, C, D) and are estimates of relative soil infiltration rates. Group A soils have the highest soil infiltration rates, while Group

D soils have the lowest. Group D also may indicate soils that are a short distance to an impermeable geology layer or that have high groundwater tables. For this study, we reclassified the hydrologic groupings as 4 (A), 3 (B), 2 (C) and 1 (D). We summarized the area-weighted value within the local catchment and also found the minimum area-weighted value of any local catchment upstream of a given reach. The upstream minimum hydrologic soil grouping was calculated to identify reaches that may drain high elevation groundwater resources impounded by dikes that are often spatially correlated with soil grouping D in perennial streams (i.e., rocky outcrops; Lau & Mink, 2006). 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. We also calculated percent of wetlands within a local catchment using data from the Coastal Change Analysis Program (CCAP; NOAA, 2005).

Rainfall

Average monthly rainfall values were available as raster data sets for the years 1992 to 2007 and were developed using a network of rainfall gages across Hawaii at a resolution of 250 m (Frazier et al., 2015). We first attributed monthly and annual rainfall values to local catchments and aggregated rainfall values within the upstream catchment for each reach. For local catchments that extended above 1830 m in elevation, we calculated area weighted averages only within the area of local catchments below 1830 m and also excluded any local catchments located completely above 1830 m (Strauch et al., 2015). This step was taken to account for the presence of the tradewind inversion layer (TWI), which results in extremely dry conditions at high elevations on Hawaii Island and Maui where potential evapotranspiration exceeds rainfall (Ehlmann et al, 2005; Erasmus, 1986). Seventy rainfall metrics (Table 1.1) were then calculated within local and upstream catchments that described monthly, wet season (May through
October), dry season (November through April) and annual rainfall average amounts; variability in rainfall across months and years; and ratios between wet and dry season rainfall.

Stream flow metrics

We downloaded daily stream flow data from the USGS National Water Information System (http://waterdata.usgs.gov/nwis) for 24 stream gages in the study region that had at least 10 years of continuous flow data from 1992-2007, with no more than five consecutive days of missing data and that occurred along perennial stream reaches represented in the HFHP stream layer. We then used the Hydrologic Index Tool (HIT; Henriksen et al., 2006) to generate 26 stream flow metrics selected based on their ability to describe different characteristics of the flow regime in flashy perennial or runoff streams (Table C1.1.; Olden & Poff, 2003). We also calculated eight additional metrics summarizing average values and variability in flow during Hawaii's wet and dry seasons, resulting in a final set of 34 stream flow metrics describing magnitude, frequency, timing, duration and rate of change of streamflow.

Biological data

Data characterizing distributions of native stream taxa collected by state researchers from 1992 to 2010 were provided by the Hawaii Division of Aquatic Resources. Presence/absence data were collected using standardized visual surveys (Higashi & Nishimoto, 2007) from streams located across the five main Hawaiian Islands, and sampling locations were attributed to reaches of the HFHP stream layer for analysis. A total of 403 perennial stream reaches were attributed with data, and in some cases, a single reach was attributed with multiple samples collected at different times during the study period. In these cases, we characterized taxa presence within a reach based on a taxa representation in at least one sample (following Steen et al., 2008). The final dataset used to classify stream reaches characterizes current distributions of nine native

stream taxa including five amphidromous fish species, two freshwater shrimp species, a neritid gastropod species, and two Kuhliidae fish species that periodically access streams from the nearshore marine environment (Table 1.2). The two Kuhliidae species were included as a single grouping in our analysis because they were only recently reclassified as two unique species (McRae et al., 2011).

Identifying variables associated with distributions of stream organisms

We reduced the initial set of 82 natural landscape variables using a series of data reduction steps specific to variable types to identify a parsimonious set of landscape variables for use in the classification. Prior to data reduction, all natural landscape variables were log(x+1) transformed (following Wang et al., 2001).

Identifying rainfall variables correlated with stream flow metrics

We used principal components analysis (PCA) to identify sets of variables that were similar in the rainfall dataset and to select a parsimonious set of variables that were minimally redundant. We used the statistical program SPSS to generate PCs from the rainfall variable correlation matrix and implemented a Varimax rotation to increase interpretability of the PCs. We selected one highly-loaded rainfall variable from each PC with λ >1 and examined Pearson's correlation coefficients with stream flow metrics to identify variables that had strong relationships (r≥|0.6|) with stream flow characteristics. Those rainfall variables that had the strongest relationships with flow were used in the reach classification.

Identifying landscape variables important to distributions of stream organisms

To identify a subset of natural landscape variables showing strong associations with stream taxa, we ran a forward selection canonical correspondence analysis (CCA) with the program CANOCO. Forward selection CCA is an ordination technique commonly used in ecological studies to identify a subset of factors explaining variation in a set of dependent variables. In our study, we used forward selection CCA to identify those variables that explained a significant (p < 0.10) amount of variation in the biological dataset (Wang et al., 2003; Esselman & Allan, 2010).

Ecological classification of stream reaches

Conditional inference tree analysis

We used conditional inference (CI) trees to develop groupings of stream reaches based on relationships between natural landscape variables and native stream taxa distributions. CI trees are a recursive partitioning technique that aims to maximize differences among groups based on differences in a set of predictor variables. We chose to use CI trees for two reasons. First, CI trees allow for generating groupings based on relationships between multiple predictor variables and multiple binary responses (Hothorn et al., 2006). Second, CI trees address two common criticisms of tree-based analyses, overfitting of trees 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 stream catchment landscape variables and the taxa distributions within study reaches. The 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, 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 competitor splits at each node to identify whether additional significant relationships between natural landscape variables and taxa

distributions were present. Examining competitor splits in recursive partitioning analysis can allow researchers to create more simplistic or meaningful trees and gain a greater understanding of observed relationships (De'ath & Fabricius, 2000). Competitor splits can suggest the influence of alternative predictor variables that also have significant relationships with the response dataset at a given node. In some instances, multiple variables could be identified as predictors at a single break; ctree defaults to selecting the variable with the lowest p-value. In our study, examining competitors in the context of current information on Hawaii streams systems allowed for the potential selection of those that are most ecologically relevant. *Validation of conditional inference tree results*

To evaluate 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. AUC can be used with binary data to select among a set of competing models or to validate the effectiveness of the model using a withheld dataset and has been used to examine the predictive capabilities of conditional inference trees and other recursive partitioning techniques (e.g., Zipkin et al., 2012; Blank & Blaustein, 2014). Individual AUC scores were calculated for each reach class using the R program ROCR (Sing et al., 2005).

Finalizing reach classes and examining taxa associations

We used the output of the CI tree as the basis for development of an ecological stream classification of the 4,732 perennial stream reaches in Hawaii. In addition to the CI tree results, three additional reach classes were created to account for established ecological relationships between natural landscape variables and distributions of native stream taxa. Stream taxa associated with each reach class were identified by comparing the percent taxa occurrence within a given class with their percent occurrence across all sampled reaches (Liu et al., 2005). Taxa

were considered associated with a particular reach class when percent occurrence was greater in the reach class than across all sampled reaches.

Results

Study site description

Many of the natural landscape features were similar in catchments of perennial stream reaches with biological samples and catchments of all perennial streams of the five main Hawaiian Islands (Table 1.3). Mean upstream catchment area was similar in reaches with samples vs. all reaches (15.9 vs. 18.7 km², respectively), as was downstream main channel slope (9.81% in reaches with samples vs. 9.09% in all reaches). Average upstream mean annual rainfall was similar among reaches with and without biological samples (3298 and 3416 mm/year, respectively). The only factors that were substantially lower in sampled reaches vs. the larger set of perennial reaches included distance inland (3797 vs. 8816 m) and minimum stream elevation (154 vs. 353 m). These differences reflect the fact that biological samples were not typically collected in difficult-to-access headwater reaches.

The goby *Awaous stamineus* was the most common taxa found in Hawaiian streams, occurring in nearly half of all sampled stream reaches (46%; Table 1.2). Two gobies (*Lentipes concolor* and *Sicyopterus stimpsoni*) and one species of atyid (*Atyoida bisulcata*) were found in just over one third of all sampled stream reaches (38, 35 and 36%, respectively). The prawn *Macrobrachium grandimanus* and goby *Stenogobius hawaiiensis* were least common and were found in only 5 and 6% of sampled stream reaches, respectively. The amphidromous neritid snail, *Neritina granosa*, was found in 24% of sampled reaches. All taxa were observed in streams on Maui, Hawaii, Oahu, and Kauai, while only five of the nine were sampled in Molokai streams (Table 1.2).

Identifying variables associated with distributions of stream organisms

The first eight principal components (PCs) of the rainfall dataset had λ >1 and accounted for 93.8% of the total variance (Table C1.2). Variables describing magnitude and variability of annual, seasonal, and monthly rainfall summarized in the local catchment had the highest loadings on PC1. Rainfall variables with high loadings on PC2 included total annual rainfall in the upstream catchment along with other upstream catchment summaries of annual, seasonal, and monthly rainfall. Variables describing variability in rainfall in the wet and the dry season across years had high loadings on PC3 and PC4, respectively. Variables describing annual variability in rainfall during February in the local and upstream catchment were strongly weighted on PC5. Variables most strongly weighting PCs 6 through 8 included annual variability in rainfall during August, April and March, respectively. We selected one rainfall variable from each of the eight PCs with a high individual loading for use in the correlation analysis with stream flow metrics (Table C1.3.).

Five flow metrics (annual runoff, wet season runoff, maximum monthly flow for August, maximum monthly runoff during the dry season, and maximum monthly runoff during the wet season) had strong correlations ($r \ge |0.60|$) with at least one of the rainfall variables identified through the PCA (Table C1.3.). The variable selected from PC2, upstream mean annual rainfall, had strong positive correlations with all five metrics. Maximum monthly dry season runoff also had a strong negative correlation with yearly variability in August rainfall. We included only upstream mean annual rainfall in the set of natural landscape variables for further consideration given its strong relationship with multiple metrics describing stream flow magnitude and a lack of additional unique relationships between stream flow metrics and other rainfall variables.

Overall, 26% of the total variance in the biological dataset was explained by the 11 landscape variables included in the forward selection CCA. Of the explained variance, 94% was attributed to 7 landscape variables: upstream catchment area, local reach slope, downstream main channel slope, reach elevation, maximum waterfall height in the downstream main channel, minimum hydrological soil grouping, and mean annual rainfall (Table 1.1). Local and upstream soil erodibility, local hydrologic soil grouping and distance inland did not explain a significant amount of variance and were not used in the generation of 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 (Figure 1.2; Table 1.4). Minimum elevation had the strongest association with taxa distributions at three nodes (values at which the CI tree splits into two subsequent groups of reaches) within the CI tree, generating splits within the dataset at 22, 76, and 231 m (nodes I, II, and VII, respectively). Downstream main channel slope had the strongest relationship with the biological dataset in low elevation reaches ($22 > X \le$ 76 m). Stream reaches above 76 m in elevation and with minimum hydrologic soil grouping values greater than 1 (i.e., excluding soil grouping D) were grouped into reach classes delineated by differences in upstream mean annual rainfall. In a single instance, a competitor variable (upstream mean annual rainfall; Node VIII) was chosen to replace the original split variable (local slope).

Validation of conditional inference tree results

Overall, AUC values suggest the analysis was effective at delineating reaches into classes based on relationships between taxa distributions and landscape variables (Table 1.4). AUC

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). The AUC values generated from the validation dataset ranged from fair (0.71) to very good (0.94) and had an average value of 0.84.

Final stream reach classes and associated taxa

Stream reach classes J, L and K were based on known ecological information of Hawaiian streams. First, reach class J was created for reaches with terminal waterfalls (falling directly to the ocean). Reaches with terminal falls are known to exclude all non-climbing organisms and to limit moderate climbers (Nishimoto & Fitzsimons, 2006) but were not well represented by sites sampled for biology. Two hundred and sixty reaches with terminal falls from reach classes A-E were grouped into reach class J. We also created an additional reach class (L) for reaches with a minimum elevation greater than 750 m. At very high elevations, stream taxa considered in this study are not often observed, likely due to limitations on upstream migration (Polhemus et al., 1992). Finally, from a subset of reaches classed as L, we created a final reach class (K) to represent high elevation bogs, a unique habitat of interest to local managers. High elevation bogs are found in several mountainous regions of Hawaii with high rainfall (Polhemus, personal communication). Class L reaches with annual rainfall values greater than 2500 mm and with more than 5% of a local catchment classified as wetlands were changed to reach class K. Six hundred and forty-four reaches from classes G, H, I and F were grouped into reach class L, while 168 from reach were grouped into reach class K.

The number of taxa associated with each reach class varied from 7 (reach class A) to 0 (G; Table 1.4). The most common taxa associated with reach classes were the atyid *A. bisulcata* (E, F, H, I, J) and the goby *Awaous stamineus* (A, B, C, D, E). Two goby species with limited

climbing abilities, *S. hawaiiensis* and *E. sandwicensis*, were associated with only a single reach class (A). The goby species *L. concolor* and *S. stimpsoni* were associated with reaches with high downstream main channel slopes. In general, number of taxa associated with a given reach class declined with increasing elevation and with lower mean annual rainfall.

Representation of reach classes across islands

Our results suggest that a diversity of stream habitats exists across the Hawaiian Islands (Figure 1.3). On the island of Oahu, low-gradient, low-elevation stream habitat is common, and 18.7% of total stream perennial stream length is classified as class A (Table 1.5). Reach class C is more prominent on the islands of Hawaii, Maui, and Molokai, while reach class B is more common 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 classes H and I, while the western half is dominated by reach classes D, E, and F. Reach classes G and L were most common across the entire study area (17.0% of total stream length). Kauai is dominated by reach class F in catchments that extend to high elevations near the center of the island. Headwater streams (reach class L) are found across all islands and make up the highest proportion of perennial stream reaches on Maui (23.7% of total stream length). Together, these results present a holistic view of habitat diversity across Hawaiian Islands at a fine spatial scale.

Discussion

In this study, we developed a classification of Hawaiian perennial stream reaches based on identified influences of natural landscape features on distributions of stream taxa. Natural landscape variables identified as having significant associations with stream taxa distributions included several known to influence aquatic biota in many stream systems. These included rainfall, groundwater delivery and channel slope. Further, others are more commonly associated

with changes in taxa distributions in regions similar to Hawaii. Elevation was one such variable, and results of our classification support current understanding of Hawaiian stream ecology and indicate that reach elevation strongly controls taxa distributions in Hawaii. Besides identification of important influences on organisms, the specific landscape variable split values identified within the CI tree allowed for generation of unique reach classes. Because these classes reflected influences of landscape on biology, they are suggestive of not only potential differences in habitat across reaches but they also provide insight into unique taxa assemblages. When applied across the entire study area, the classes provide a representation of ecological potential for all stream reaches in Hawaii and allow for identification of common and rare habitats at the reach scale, which has particular relevance for conservation prioritization decisions in Hawaii.

Landscape variables strongly associated with stream taxa distributions

Several of the natural landscape variables identified through the CCA that have strong associations with the biological dataset, including local channel slope (e.g., Walters et al., 2003; Infante et al., 2006; Maret et al., 2007), mean annual rainfall (e.g., Derolph et al., 2014), and hydrologic soil grouping (Stauffer et al., 2000; Brewer et al., 2007), have been shown to influence biology in streams in other regions. However, some natural landscape variables that had strong associations with the biological dataset are more regionally specific. Elevation and downstream maximum waterfall height are associated with differences in species composition in tropical island streams and have been used to broadly describe patterns in species assemblages (Polhemus et al., 1992; Parham & Lapp, 2006). In addition, in streams of New Zealand where migratory species are also 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 streams ability to support aquatic biota.

Ecological classification of stream reaches

Influences of landscape variables on stream taxa distributions

The results of the CI tree yielded richer insights into the influence of landscape features on stream taxa distributions. Among the natural landscape variables examined in this study, the elevation at the terminal point of a given reach 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 m and 231 m) are similar to those used to broadly classify Hawaiian streams into biological zones (20 m and 200 m; Parham & Lapp, 2006), linking the results of the classification to current understanding of taxa distributions in Hawaii. The presence of an additional elevation split (76 m) suggests that our results further define the influence of elevation on taxa distributions in Hawaii, separating climbing taxa from non-climbing. The importance of elevation in defining stream reach classes is likely the result of differing abilities of individual taxa to ascend step reaches (Polhemus et al., 1992; Nishimoto & Fitzsimons, 2006) and is reflected by the taxa associated with each reach class. For instance, the association of L. concolor and A. bisulcata with highest elevation reach classes is likely due to their abilities to traverse most natural barriers in Hawaii. Similarly, the association of nearshore and nonclimbing taxa with low elevation classes suggests that with increasing elevation the location of a single migratory barrier along the stream network prevents further upstream migration.

We also found that reach classes with higher channel slopes were associated with a greater number of taxa 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 relatively higher gradient reaches can therefore have larger substrate than lower gradient reaches (Knighton, 1998). In streams of Michigan, higher channel slope was also associated with greater habitat complexity independent of its effect on stream power, which in turn had positive influences on species richness (Infante & Allan, 2010). 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. Large substrate composition 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, 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 low gradient reaches. This may be due to a habitat preference for deep and slow pools where A. stamineus forages for macroinvertebrates by burrowing within fine sediments, a unique feeding strategy not practiced by other Hawaiian gobies (Kinzie & Ford, 1982; Kinzie, 1988).

Our results also indicate that the amount of rainfall that occurs within a catchment influences the habitat of Hawaiian stream reaches. This is not surprising, as mean annual rainfall was positively correlated with measures of stream flow magnitude in this study and likely reflects broad differences in total available habitat and the likelihood that a stream experiences very low flow or drying events. However, the CI tree results also indicate that effects of rainfall on taxa distributions are most important in systems with less potential groundwater delivery (as indicated by upstream minimum hydrologic soil grouping). 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. On each island, changes in reach class and subsequent declines in associated taxa occur with increasing elevation and are represented by the classification. A higher percentage of lower elevation, lower gradient reach classes on Oahu and Kauai indicates that the majority of habitat associated with nonclimbing and nearshore taxa occur on these islands. Reaches at moderate to high elevation on the Hilo/Hamakua coast of Hawaii Island as well as eastern Maui consist predominantly of classes more dependent on rainfall to support stream flow, suggesting that stream habitat in these regions may be more vulnerable to declines in mean annual rainfall that may occur with climate change. The overall change in dominant reach classes at moderate to high elevations from east to west along the island chain is indicative of changes in groundwater delivery. Streams on older islands with greater channel incision are more likely to be influenced by dike impounded groundwater that contributes to baseflow (Craig, 2003; Lau & Mink, 2006; Izuka et al., 2015).

The extrapolation of the classification to all reaches across the study area allows for the consideration of how additional biological surveys or spatial data layer development can help further delineate unique classes and increase our understanding of Hawaiian stream ecology. For instance, additional breaks within reach class D associated with waterfall height or increases in elevation may distinguish additional differences in taxa distributions, but high elevation reaches

are underrepresented in the biological dataset due to limited access and higher cost of sampling. Similarly, increased biological sampling in low elevation streams with limited groundwater input across a gradient in rainfall may also indicate whether differences in taxa associations observed in classes at moderate to high elevations (I, H, and G) are mirrored in some lower elevation reaches (C and J). In addition, while the relationships between upstream minimum hydrologic soil grouping and taxa distributions are related to differences in the influence of groundwater on baseflow and may be better represented with additional data that represents groundwater resources not captured by minimum hydrologic soil grouping (i.e., perched groundwater; Izuka et al., 2015).

Utility of the analytical approach

We conducted the Hawaii stream reach classification using an approach that considered the natural landscape characteristics of an individual reach regardless of its location within the study area. This place-independent approach can delineate differences among reaches that may not be represented by classification approaches that begin by clustering rivers in large or multiple catchments (Leathwick et al., 2011). While a potential limitation of place-independent approaches is the lack of consideration of directional connectivity of stream systems, our study accounted for this directional relationship by including natural landscape variables summarized in upstream catchments.

We acknowledge that human disturbance is likely to have some influence on the distribution of stream organisms in Hawaii. However, in similar ecological classifications, the influence of disturbance is acknowledged, but the potential of streams to support taxa is considered in the context of just natural landscape factors (i.e., Brenden et al., 2008). In addition, we assert that the potential bias from landscape disturbance is limited within the

biological distributions represented by our data. This results from two factors. First, a recently completed Habitat Condition Index of Hawaii indicates that 80% of sampled reaches used to generate the classification have very low to moderate risk of disturbance from current anthropogenic sources (Tsang et al., in preparation), suggesting that the influence of disturbance on the presence of native taxa is limited within the dataset. In addition, the amphidromous life history and the presumed lack of natal stream homing (Chubb et al., 1998; McDowall, 2003; Bebler & Foltz, 2004) of native stream taxa results in an open population in which individuals are likely to migrate into both "source" and "sink" stream reaches (McRae, 2007). This continuous influx of new individuals suggests that even in degraded stream reaches, native taxa may be represented in presence/absence datasets.

Taxa associated with each reach class offer a useful biological characterization of a given reach. For instance, the lack of a taxa association with a reach class, such as the absence of nonclimbing taxa in reaches above 76 m in elevation, is a strong indication that taxa are not capable of accessing areas above this elevation and can be accepted with confidence. However, in other instances the lack of an association may be the result of low occurrence of the taxa overall in the biological dataset. For example, *S. hawaiiensis* and *E. sandwicensis* are not associated with reach class B, despite substantial overlap in habitat preference of these two taxa with *A. stamineus* (McRae et al., 2013). Therefore, taxa association for a specific reach class should be considered in the context of available ecological knowledge.

Utility for conservation

Classifications are most useful when they incorporate and add to current understanding of ecology and are built to address specific objectives. In Hawaii, endemic shrimp, 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 conservation decision making. 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. The classification can also be paired with human disturbance datasets and habitat condition indices to assess which habitats and taxa are at particular risk from human disturbance. A similar approach can be used to assess Hawaiian stream vulnerability to climate change by utilizing downscaled projected climate change data to assess how streams may experience shifts in reach class under the influence of climate change and variability. Beyond assessment of disturbance or change within and among reach classes, finer-resolution biological data (i.e., abundance data, disease prevalence, growth rates of individuals in different habitats) can be examined within or across classes associated with particular taxa to assess how disturbances may affect stream populations. This information can then be used to improve understanding of the potential effects of climate change on stream organisms, for example in the case of reduced or more variable streamflow.

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 understand the ecological potential of Hawaiian streams. The selection of some variables that are known to influence species distributions in many regions as well as the selection of some variables that are more regionally specific suggest that continued research on

the relationships between the landscape, habitat and biota in understudied regions is required to fully characterize differences in habitat across large spatial extents.

Our application of a quantitative analytical approach that identifies relationships between the landscape and stream taxa supported the development of a study area-wide classification of streams that includes reaches where habitat or biological data are not available but a spatial understanding of stream resources is needed to inform conservation. We chose to conduct our study in Hawaii to demonstrate the value of such an approach in understudied regions like tropical islands of the Pacific, which support many endemic organisms that are threatened by disturbance from anthropogenic land use and climate change. However, we believe the 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 and poorly understood relationships with stream habitat and biota. **APPENDICES**

APPENDIX 1.A

Tables

Table 1.1. Landscape variables considered for use in the Hawaiian stream classification. Variables were summarized at three spatial scales: local (L), upstream (U) and downstream main channel (D) catchments. Individual variables were summarized at multiple spatial extents, resulting in 82 natural landscape variables. Asterisks (*) indicate the eleven natural landscape variables included in the CCA. Two asterisks (**) indicate the variables that explained a significant amount of variation within the biological dataset.

				Spatial
Category	Code	Variable description	Units	scales
Stream siz	ze and channel s	lope		
	AREAKM	Upstream catchment area	km ²	U**
	SLOPE	Reach slope	%	L**
	MC_SL	Main channel slope	%	D**
Influences	s on migration			
	MIN_ELE	Reach elevation	m	L**
	DIST_IN	Reach distance inland	m	L*
	DROP_WF	Maximum waterfall height	m	D**
	EROD	Soil erodibility	•	U*,L*
Soil chara	cteristics			
	HY	Hydrologic soil grouping	•	L*
	MIN_HY	Minimum soil grouping	•	U**
	WETLAND	Wetland land cover	km ²	U,L
Rainfall				
	MAR	Mean annual rainfall	mm/yr	U**,L
	D	Mean dry season rainfall	mm/yr	U,L
	W	Mean wet season rainfall	mm/yr	U,L
	(1-12)	Mean monthly rainfall	mm/yr	U,L
	MAR_VAR	C.V. ¹ of mean annual rainfall	mm/yr	U,L
	D_VAR	C.V. ¹ of mean dry season rainfall	mm/yr	U,L
	W_VAR	C.V. ¹ of mean wet season rainfall	mm/yr	U,L
	MM_VAR	Mean C.V. ¹ of monthly means	mm/yr	U,L
	(1-12)_VAR	C.V. ¹ of rainfall for a given month	mm/yr	U,L
	WD_RAT	Ratio of total wet to dry season rainfall	mm/yr	U,L

¹Coefficient of variation

			Sampled	Present in sampled reaches					
Taxa	Common name	Taxa code	reaches where taxa occur (%)	Hawaii	Maui	Molokai	Oahu	Kauai	
Aytoida bisulcata	'opae kala'ole	1	38	Y	Y	Y	Y	Y	
Lentipes concolor	o' opu alamo'o	2	35	Y	Y	Y	Y	Y	
Sicyopterus stimpsoni	o' opu nopili	3	36	Y	Y	Y	Y	Y	
Awaous stamineus	o' opu nakea	4	46	Y	Y	Y	Y	Y	
Neritina granosa	hihiwai	5	24	Y	Y	Y	Y	Y	
Eleotris sandwicensis	o' opu 'akupa	6	12	Y	Y	Ν	Y	Y	
Stenogobius hawaiiensis	o 'opu nahina	7	6	Y	Y	Ν	Y	Y	
Macrobrachium grandimanus	opae oeha'a	8	5	Y	Y	Ν	Y	Y	
Kuhlia sp.	āholehole	9	13	Y	Y	Ν	Y	Y	

Table 1.2. Stream taxa used in the ecological classification of Hawaiian streams

				90^{th}	10^{th}
Category	Variable	Mean	Median	percentile	percentile
All perent	nial 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 (m)	8816.55	6505.10	161.20	21473.47
	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/yr)	3298.18	3150.00	1600.00	5232.00
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 elevation (m)	154.48	95.00	21.00	370.00
	Distance inland (m)	3797.36	2535.15	724.74	8827.81
	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/yr)	3416.39	3429.00	2108.00	5100.00

Table 1.3. Descriptive statistics for all natural landscape variables summarized for perennial stream catchments across the study region (n=4,732) and for those with biological samples (n=403).

Reach		Validation	
class	Description	AUC	Associated taxa
A	Coastal	0.73	S. stimpsoni, A. stamineus, N. granosa, E. sandwicensis, S. hawaiiensis, M. grandimanus, Kuhlia sp.
B^*	Low gradient downstream channel at low elevation	N/A	A. stamineus, M. grandimanus
С	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, potential high water table	0.90	A. stamineus, S. stimpsoni
E	High gradient, moderate elevation, potential high water table	0.91	A. bisulcata, L. concolor, S. stimpsoni, A. stamineus, N. granosa
F	High gradient, high elevation, potential high water table	0.88	A. bisulcata, L. concolor
G	Moderate to high elevation, low rainfall	0.71	
Н	Moderate to high elevation, moderate rainfall	0.87	A. bisulcata
Ι	Moderate to high elevation, high rainfall	0.94	A. bisulcata, L. concolor
J	Terminal falls at low elevation	N/A	A. bisulcata, L. concolor
Κ	High elevation bogs	N/A	
L	Headwater streams	N/A	

Table 1.4. Descriptions, area under the curve (AUC) for validation datasets, and associated taxa for each stream reach class.

*AUC was not calculated for the validation dataset of reach class B due to low sample size

Reach	All					
class	islands	Hawaii	Maui	Molokai	Oahu	Kauai
А	7.4	2.5	3.4	4.5	18.7	9.0
В	5.0	0.6	0.2	3.7	11.5	8.5
С	4.5	6.5	8.3	6.2	1.6	2.0
D	12.5	0.3	2.4	3.7	39.7	17.3
Е	3.8	0.7	4.5	12.4	4.7	5.5
F	11.4	3.7	14.4	36.6	8.9	17.0
G	17.0	24.2	8.1	5.2	8.3	18.2
Н	6.1	9.2	13.5	2.3	2.7	2.0
Ι	8.7	17.6	16.2	1.1	2.5	0.0
J	3.3	7.6	2.8	0.9	0.0	0.5
Κ	3.3	0.0	2.5	19.9	0.0	6.8
L	17.0	27.0	23.7	3.5	1.4	13.3

Table 1.5. Percent of the total stream length across and within individual islands of each reach class.

APPENDIX 1.B

Figures



Figure 1.1. Study area and locations with biological data.



Figure 1.2. 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 that create significant splits in species distributions.



Figure 1.3. Final classification of Hawaiian stream reaches.

APPENDIX 1.C

Supplemental tables

Category	Code	Description
Magnitude	e	
	MA10	Range in daily flow (20th/80th) divided by median daily flows
	MA26	Coefficient of variation of March flows
	MA41	Mean annual runoff
	MA46*	Average of dry season runoff (May-September)
	MA47*	Average wet season runoff (November-March)
	MA48*	Coefficient of variation of flows during dry season
	MA49*	Coefficient of variation of flows during dry season
	ML14	Mean of annual minimum flows
	ML16	Median of annual minimum flows
	ML17	Baseflow index
	ML23*	Mean minimum yield in dry season
	ML24*	Mean minimum yield in wet season
	MH8	Mean maximum monthly flow for August
	MH14	Median of annual maximum flows
	MH28*	Mean maximum yield in dry season
	MH29*	Mean maximum yield in wet season
	MH23	High flow volume
Frequency	7	
	FL2	Variability in low flood pulse count
	FL3	Frequency of low flow spells
	FH4	High flood pulse count
	FH6	Flood frequency (threshold 3x median flow)
	FH7	Flood frequency (threshold 7x median flow)
Duration		
	DL6	Variability in annual minima of daily discharge (one day)
	DL10	Variability in annual minima of daily discharge (90 day)
	DL17	Variability in low flow pulse duration
	DH13	Means of 30 day maxima of daily discharge
	DH16	Variability in high flow pulse duration
	DH24	Flood free days
Timing		
-	TA1	Constancy
	TA2	Predictability of flow

Table C1.1. Hydrological metrics calculated from Hydrological Index Tool and seasonal metrics calculated for the wet and dry seasons (denoted with *). Hydrological Index Tool metric descriptions follow Olden & Poff (2003).

Table C1.1 (cont'd).

Category	Code	Description
Timing		
	TH3	Seasonal predictability of non-flooding
Rate of ch	ange	
	RA6	Change of flow (increasing)
	RA7	Change of flow (decreasing)
	RA9	Coefficient of variation in reversals

Rainfall variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Variance (%)	53.47	17.35	7.37	6.33	3.60	2.41	1.83	1.45
L_mar	0.92*	0.37	-0.02	-0.05	-0.04	-0.01	-0.02	-0.03
L_m_d	0.92*	0.35	-0.05	-0.07	-0.03	-0.08	-0.12	-0.04
L_mwr	0.92*	0.37	0.01	-0.04	-0.04	0.05	0.06	-0.01
L_m_1	0.86*	0.41	-0.08	-0.08	0.04	0.15	0.18	0.03
L_m_2	0.90*	0.36	-0.06	-0.02	-0.09	0.07	0.06	-0.01
L_m_3	0.91*	0.34	0.07	-0.10	-0.05	0.08	0.11	0.00
L_m_4	0.92*	0.30	0.07	-0.12	-0.08	-0.10	0.03	-0.02
L_m_5	0.92*	0.35	-0.01	-0.13	0.02	-0.06	-0.05	-0.04
L_m_6	0.91*	0.30	-0.09	-0.06	-0.06	-0.08	-0.14	-0.05
L_m_7	0.91*	0.33	0.04	-0.12	-0.02	-0.15	-0.11	-0.11
L_m_8	0.91*	0.32	0.01	-0.09	0.00	-0.16	-0.17	-0.04
L_m_9	0.89*	0.36	-0.09	-0.04	-0.02	-0.08	-0.18	-0.03
L_m_10	0.88*	0.40	-0.19	0.00	-0.07	0.06	-0.07	0.00
L_m_11	0.90*	0.39	-0.02	0.07	-0.02	0.08	-0.05	-0.04
L_m_12	0.90*	0.39	-0.02	-0.02	-0.02	0.04	0.06	-0.01
L_mar_var	-0.71*	-0.30	-0.05	0.32	0.31	0.27	0.14	0.22
L_m_d_var	-0.26	-0.18	0.91*	0.06	0.16	-0.07	0.05	0.09
L_m_w_var	-0.59	-0.33	0.02	0.39	0.37	0.22	-0.09	0.32
L_m_1_var	-0.26	0.39	0.37	0.68*	0.21	0.04	0.00	-0.19
L_m_2_var	-0.46	0.07	0.35	0.13	0.72*	-0.18	-0.04	-0.04
L_m_3_var	-0.42	-0.42	-0.31	0.22	-0.15	0.00	0.09	0.66*
L_m_4_var	-0.57	-0.30	0.35	0.14	0.00	-0.21	0.51	0.19
L_m_5_var	-0.24	-0.25	0.74*	0.29	-0.18	0.00	-0.01	0.23
L_m_6_var	-0.11	-0.07	0.89*	0.06	0.12	0.11	0.24	-0.03
L_m_7_var	-0.23	-0.05	0.81*	0.01	0.36	-0.04	-0.28	0.14
L_m_8_var	-0.70*	-0.23	0.33	0.12	0.19	0.33	0.00	0.23
L_m_9_var	-0.45	-0.16	0.66*	-0.04	0.10	-0.27	0.23	-0.25
L_m_10_var	-0.51	-0.08	0.76*	0.10	0.29	-0.04	0.07	-0.02
L_m_11_var	-0.22	-0.13	0.15	0.91*	0.05	0.07	0.01	0.12
L_m_12_var	-0.78*	-0.24	-0.14	0.03	0.26	0.11	0.28	0.29
L_mm_var	-0.73*	-0.24	0.35	0.32	0.05	0.16	0.33	0.16
L_d_mm_var	-0.71*	-0.20	0.52	0.19	0.00	0.18	0.26	0.12
L_mm_w_var	-0.62*	-0.20	0.28	0.56	0.19	-0.05	0.22	0.26

Table C1.2. The eight principal components (PCs) generated from rainfall variables with $\lambda > 1$ explained 93.8% of the total variance. PC loadings $\geq \pm 0.60$ are denoted by an asterisk.

Table C1.2. (cont'd)

Rainfall variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
L_wd_rat	-0.72*	-0.24	0.33	0.10	0.02	0.26	0.38	0.10
L_wd_rat_std	-0.47	-0.17	0.72*	0.11	0.07	0.12	0.20	0.14
U_mar	0.52	0.83*	-0.15	-0.05	-0.02	-0.06	-0.08	-0.06
U_d	0.50	0.81*	-0.17	-0.08	0.04	-0.15	-0.16	-0.06
U_w	0.53	0.83*	-0.13	-0.04	-0.06	0.01	0.01	-0.06
U_1	0.34	0.85*	-0.26	-0.08	0.04	0.15	0.14	-0.02
U_2	0.56	0.78*	-0.18	-0.06	-0.10	0.04	0.03	-0.03
U_3	0.51	0.83*	0.02	-0.10	-0.04	-0.01	0.06	-0.09
U_4	0.55	0.76*	-0.05	-0.15	-0.11	-0.22	-0.02	-0.05
U_5	0.54	0.78*	-0.15	-0.12	0.03	-0.15	-0.13	-0.05
U_6	0.42	0.81*	-0.23	-0.09	0.03	-0.16	-0.13	-0.06
U_7	0.48	0.78*	0.00	-0.14	0.07	-0.28	-0.15	-0.14
U_8	0.52	0.77*	-0.06	-0.08	0.11	-0.21	-0.24	-0.04
U_9	0.49	0.80*	-0.23	-0.04	0.05	-0.10	-0.19	-0.03
U_10	0.46	0.79*	-0.38	0.00	-0.04	0.04	-0.11	-0.03
U_11	0.57	0.77*	-0.16	0.11	-0.04	0.06	-0.11	-0.08
U_12	0.47	0.84*	-0.19	-0.01	-0.06	0.04	0.01	-0.04
U_mar_var	-0.28	-0.53	-0.00	0.42	0.28	0.49	0.21	0.12
U_d_var	0.24	-0.15	0.92*	0.11	0.03	0.02	-0.03	-0.07
U_w_var	-0.22	-0.52	0.16	0.47	0.40	0.34	-0.12	0.23
U_1_var	0.06	0.38	0.37	0.73*	0.15	0.14	-0.01	-0.22
U_2_var	-0.08	0.06	0.42	0.23	0.77*	0.10	-0.08	-0.11
U_3_var	-0.28	-0.63*	-0.25	0.19	-0.12	0.00	0.04	0.59
U_4_var	-0.26	-0.44	0.42	0.09	-0.21	-0.03	0.63*	0.01
U_5_var	0.07	-0.30	*0.74	0.30	-0.32	0.11	-0.02	0.03
U_6_var	0.29	0.06	*0.83	0.05	0.02	0.19	0.18	-0.24
U_7_var	0.31	0.04	*0.78	0.04	0.28	0.05	-0.31	0.00
U_8_var	-0.10	-0.17	0.30	0.30	-0.01	0.78*	-0.08	-0.03
U_9_var	0.01	-0.11	*0.78	0.11	-0.11	-0.03	0.34	-0.31
U_10_var	-0.09	-0.12	*0.87	0.14	0.20	0.21	0.06	-0.08
U_11_var	0.05	-0.22	0.15	0.93	-0.03	0.08	-0.01	0.07
U_12_var	-0.51	-0.47	-0.15	0.12	0.32	0.27	0.27	0.35
U_mm_var	-0.21	-0.49	0.52	0.46	-0.12	0.33	0.30	0.05
U_mm_d_var	-0.13	-0.34	0.67*	0.25	-0.18	0.44	0.26	-0.09
U_mm_w_var	-0.16	-0.34	0.38	0.74*	0.09	0.11	0.18	0.16
U_wd_rat	-0.23	-0.58	0.43	0.13	-0.21	0.35	0.36	0.05
U_wd_rat_std	0.28	-0.01	0.86*	0.20	-0.02	-0.08	-0.25	0.00

Flow								
metric	U_mar	L_mar	U_d_var	L_11_var	L_2_var	U_8_var	U_4_var	L_3_var
MA10	0.17	0.30	0.50	0.16	-0.35	-0.46	0.33	-0.06
MA26	0.36	0.32	0.36	0.06	-0.38	-0.44	0.24	-0.29
MA41	0.66*	0.53	0.20	-0.08	-0.14	-0.56	0.46	-0.49
MA46	0.57	0.43	0.26	-0.02	0.00	-0.47	0.47	-0.46
MA47	0.68*	0.51	0.21	0.02	-0.05	-0.41	0.47	-0.47
MA48	-0.12	0.09	0.55	0.21	-0.11	-0.26	0.54	0.16
MA49	0.03	0.15	0.57	0.10	-0.22	-0.24	0.20	-0.18
ML14	-0.04	-0.17	-0.34	-0.23	0.26	0.32	-0.17	-0.11
ML16	-0.04	-0.18	-0.35	-0.22	0.27	0.31	-0.17	-0.11
ML17	-0.16	-0.21	-0.39	-0.21	0.32	0.38	-0.24	0.03
ML23	0.33	0.09	-0.18	-0.16	0.29	-0.07	0.15	-0.27
ML24	0.27	0.02	-0.27	-0.15	0.31	0.05	0.09	-0.20
MH8	0.68*	0.36	0.21	0.27	0.05	-0.27	0.18	-0.50
MH14	0.18	0.25	0.26	0.12	-0.35	-0.25	0.04	0.01
MH23	0.01	0.16	0.10	0.19	-0.21	-0.08	-0.05	0.25
MH28	0.71*	0.55	0.25	-0.03	-0.20	-0.61*	0.39	-0.50
MH29	0.69*	0.57	0.34	0.07	-0.24	-0.48	0.49	-0.47
FL2	-0.35	-0.31	-0.28	-0.23	0.20	0.34	-0.18	0.15
FL3	0.04	0.23	0.17	-0.13	-0.22	-0.43	0.16	0.17
FH4	0.19	0.27	0.45	0.16	-0.39	-0.44	0.31	-0.09
FH6	0.30	0.20	0.37	0.06	-0.37	-0.47	0.30	-0.30
FH7	0.19	0.25	0.43	0.12	-0.42	-0.45	0.29	-0.12
DL6	-0.33	-0.16	0.00	0.07	-0.15	-0.11	-0.09	0.40
DL10	-0.08	0.13	0.33	0.28	-0.14	-0.16	0.07	0.20
DL17	-0.24	-0.13	-0.36	-0.09	0.29	0.37	-0.17	0.32
DH13	0.24	0.30	0.32	0.18	-0.33	-0.40	0.21	0.00
DH16	-0.44	-0.29	-0.37	-0.05	0.32	0.39	-0.23	0.45
DH24	0.16	0.07	-0.23	-0.22	0.06	-0.09	-0.10	-0.21
TA1	0.34	0.02	-0.13	-0.06	0.23	-0.18	0.15	-0.25
TA3	-0.04	0.08	0.04	0.22	-0.18	0.13	-0.34	0.14
TH3	-0.16	0.01	0.10	0.48	0.02	0.48	0.00	0.26
RA6	0.29	0.25	0.30	-0.01	-0.40	-0.50	0.23	-0.23
RA7	0.15	0.13	0.34	0.07	-0.25	-0.40	0.16	-0.10
RA9	-0.24	-0.01	-0.31	-0.14	-0.01	-0.09	-0.20	0.21

Table C1.3. Correlations between selected stream flow metrics and rainfall variables. Highly correlated variables ($r \ge \pm 0.60$) are denoted by an asterisk (*).

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CHAPTER 2

ANTICIPATING EFFECTS OF CHANGING CLIMATE ON TROPICAL ISLAND STREAMS: INFLUENCES OF STREAM FLOW ON ATYID MOUNTAIN SHRIMP

Abstract

Climate change will alter stream flow regimes and may have negative effects on populations of stream organisms. This ultimately threatens population persistence in regions that experience changes in climate, including tropical islands, which harbor many endemic species. This study examined associations between flow regimes and population characteristics of the endemic mountain shrimp, Atyoida bisulcata, found in high elevation streams of Hawaii. We first identified aspects of the flow regime strongly associated with rainfall across a set of study streams. Then, we identified relationships between rainfall-sensitive flow metrics and stream habitat factors. Finally, we characterized relationships between rainfall-sensitive flow metrics and population characteristics of A. bisulcata. Our results showed that multiple aspects of the flow regime were strongly associated with mean annual rainfall, including baseflow, flow variability, and flow event duration and frequency, and these rainfall-sensitive flow metrics were associated with changes in available habitat type and moss and filamentous algae cover. A. *bisulcata* in streams with lower baseflows were smaller and in poorer condition than in streams with higher baseflows, and individuals in streams with higher flow variability had a greater prevalence of brown spot disease. Together, our results indicate that declines in annual rainfall leading to lower baseflow and greater flow variability may negatively affect A. bisulcata. Further, these findings demonstrate the value of considering relationships between population characteristics and stream flow metrics as opposed to presence/absence or abundance data as a way to understand how climate change could affect stream organisms, offering insights that could be used in support of proactive conservation strategies.

Introduction

The stream flow regime is a dominant factor influencing stream organisms (Poff et al., 1997). Flow regimes include flow magnitude, frequency, duration, timing and rate of change of events (Poff & Ward, 1989), all of which can differentially affect distributions and abundances of stream organisms. Reductions in stream flow magnitude and increases in duration or frequency of low flow events can change physical characteristics of the stream environment including reducing available habitat, increasing temperature and/or reducing dissolved oxygen. Such changes can increase stress to and reduce growth of organisms (as reviewed by Rolls et al., 2012), and in more extreme cases, exclude organisms entirely from streams (e.g., Canton et al., 1984). Increased frequency of high flow events may also be problematic, resulting in a temporary loss of species unable to persist during high flows (e.g., Meffe & Minckley, 1987). For some stream fishes, timing of seasonal high flows controls timing of spawning events (Lytle & Poff, 2004) and larval hatching (e.g., Naesje et al., 1995). The rate of change of stream flows also affects organisms, stranding individuals in suboptimal habitats following quick flow recessions (e.g., Bradford, 1997; Davey et al., 2006) or flushing them downstream after rapid increases in flow (Cushman, 1985).

Physical characteristics of the catchment (such as geology, topography, and land cover) as well as regional climate influence stream organisms through indirect controls on the flow regime (Poff et al., 1997). Examples of climatic controls include the total amount and timing of precipitation events as well as effects of air temperature on snowmelt and evapotranspiration. Given the influences of climate on stream flow, changes in precipitation and air temperature affect the physical habitat of streams and species they support through alterations to the flow regime. Recent studies have documented such changes in multiple regions. In snowmelt-driven

streams of the western United States over the past half century, warmer air temperatures have caused earlier snowmelts, resulting in increased winter and spring discharges and declines in summer flows (Leppi et al., 2012; Zeigler et al., 2012), reducing available habitat for native cutthroat trout (Isaak et al., 2012). In Pacific Northwest streams, more fall and winter rainstorms over the past 30 years have likely caused greater flow variability during winter months, reducing natural reproduction of Chinook salmon (Ward et al., 2015). In the Rio Grande, shorter and smaller snowmelt-driven spring discharges resulting from warmer air temperatures have been shown to reduce differences in spawning dates of eight stream fish species, potentially increasing interspecific competition among fish larvae for food (Krabbenhoft et al., 2014). Together, these studies offer important insights into diverse flow-induced ecological changes resulting from documented changes in climate.

While the studies above describe climate influences within temperate regions, we are currently aware of no studies that have documented climate effects on flow regimes and organisms in tropical island streams. This lack of information is particularly problematic for several reasons. First, changes in the magnitude and timing of rainfall are likely to occur with climate change throughout the tropics (IPCC, 2013), and reduced rainfall may alter stream flow regimes and threaten endemic species that inhabit tropical island streams (Leong et al., 2014). This is especially concerning given the fact that many tropical island streams require persistent rainfall for maintenance of baseflow (Craig, 2003). Reductions in rainfall that reduce flows could change stream habitat by increasing temperatures or lowering dissolved oxygen; in extreme cases, reductions in flow could lead to complete loss of stream habitat. An additional cause for concern is that many freshwater shrimp, fish and snails inhabiting tropical islands require hydrological connectivity to marine environments to complete amphidromous life

histories where larvae hatch in stream systems, passively drift downstream to the ocean, spend weeks to months developing in the marine environment, then use freshwater cues to migrate back upstream (Keith, 2003; Nishimoto & Fitzsimons, 2006; McDowall, 2007; Bauer, 2013). Reductions in streamflow may limit drift of larvae to the ocean and may also slow or stop juvenile migration upstream after their marine stage (Gorbach et al., 2012; Walter et al., 2012; Leong et al., 2014). Finally, stream flow reductions may change food availability by reducing available foraging space and by limiting delivery of fine particulate organic matter (FPOM) and availability of basal food resources (James et al., 2007), reducing individual growth and condition. Ultimately, changes in stream flow within tropical island systems represent a significant threat that could lead to loss of species from altered stream habitats.

In response to changes in stream flow and prior to species loss, changes are likely to occur to individual populations such as size or age structure, average body condition, disease prevalence, or fecundity. For example, reductions in growth may result from lower habitat and food availability associated with lower stream flows, which may be reflected in the average size of individual organisms. Increases in flow variability may increase stress on aquatic organisms, potentially increasing their vulnerability to disease and infection (Jones et al., 2012). In temperate streams, researchers have begun to study relationships between flow regimes and population characteristics (e.g., age structure, fecundity) to understand effects of changing climate on stream organisms operating through aspects of the flow regime (Krabbenhoft et al., 2014; Ward et al., 2015). Studies such as these remain uncommon (as reviewed by Lynch et al., 2016), yet understanding specifically how climate influences populations can provide insight into the mechanisms that may eventually result in species loss as climate change progresses.

The goal of our study is to understand how the flow regime influences population characteristics of tropical stream organisms. We focus our research on high elevation streams of Hawaii inhabited by the endemic Atyoida bisulcata, an amphidromous atyid mountain shrimp found in streams throughout the islands. A. bisulcata are listed as "near threatened" by the International Union for Conservation of Nature (IUCN; De Grave and Cai, 2013) due to their extremely limited distribution (restricted to the Hawaiian Islands) as well as their declining populations resulting from habitat loss and degradation from anthropogenic land use and water diversions (Brasher, 2003). Despite their conservation status, ecological information on A. bisulcata is limited to a single thesis (Couret, 1976) and several published reports (e.g., Nishimoto & Kauamo'o, 1996; Brasher, 1997; Gingerich & Wolff, 2005), although these studies provide little information on influences of stream flow regimes on populations. This represents a critical knowledge gap, as changes in rainfall over the last century have been linked to reductions in baseflow across Hawaiian streams (Bassiouni & Oki, 2013; Frazier & Giambelluca, 2016) and projected climate data indicate that regionally specific declines in rainfall will continue as climate change progresses over the next century (Timm et al., 2015).

Our first objective is to assess characteristics of flow regimes strongly influenced by rainfall across a set of study streams. Second, we identify relationships between those rainfall-sensitive flow metrics and select stream habitat factors to consider how changes in rainfall could affect habitat. Finally, we characterize relationships between population characteristics of *A*. *bisulcata* and those rainfall-sensitive flow metrics and habitat factors. By comparing streams with similar landscape characteristics across a wide gradient in annual rainfall, we can make inferences about how climate may affect stream biota based on identified relationships between rainfall-sensitive flow metrics and select stream habitat factors. Our results will provide insight

into how climate operates through the flow regime to influence populations of tropical island stream organisms, thereby increasing our understanding of the potential effects of climate change on these systems.

Methods

Study area

The study area is located along the North Hilo coast of Hawaii Island, where a gradient in mean annual rainfall ranging from 3000 to 7000 mm/year exists over a linear distance of less than 30 km (Giambelluca et al., 2013; Figure 2.1). We evaluated 11 first- and second-order stream reaches lying between 470 and 510 m in elevation and bounded by plunge pools created by waterfalls at their inflows and outflows (Figure 2.1; Table 2.1). Catchments draining these reaches have minimal urban and agricultural land use and are composed primarily of mixed native and non-native forests (Price et al., 2012). The streams drain land on porous volcanic geology ranging in age from 5,000 to 64,000 years (Sherrod et al., 2008) with soils that are classified as erodible and are primarily Akaka and Honokaa soil types (USDA, 1995). Recent research across our study reaches indicates that baseflow magnitude is lower and flow variability is higher in streams with lower mean annual rainfall, suggesting that flow regimes in these systems are heavily dependent on rainfall (Strauch et al., 2015). Similarities in landscape characteristics of stream catchments in our study area and the strong relationships between stream flow and mean annual rainfall make the North Hilo Coast a useful system to study linkages between climate, the stream flow regime, and stream organisms.

Data collection and processing

Mean annual rainfall

We generated estimates of mean annual rainfall from 1992-2007 for each study reach using 250-m monthly rainfall raster datasets developed by Frazier et al. (2015). We summed monthly raster datasets to create annual rainfall estimates for each of 16 years, which were then attributed to local catchments, or the area draining directly to a stream reach (Tingley, this volume a). We then summarized these yearly data in the entire landscape in the upstream stream network draining to the reach (i.e., the upstream catchment; following Wang et al., 2011) using the aggregation method described in Tsang et al. (2014). Finally, we averaged annual values to obtain a long-term estimate of mean annual rainfall at the catchment scale for each study reach. *Stream flow*

Daily stream flow data

We obtained daily stream flow records for the 2012, 2013, and 2014 water years from multiple sources. For a single study reach, Honolii, we downloaded daily flow data from the USGS National Water Information System (https://waterdata.usgs.gov/usa/nwis/16717000). We averaged daily stream flows from 15-min interval instantaneous flow data collected at gaging stations installed between spring of 2011 and fall of 2012 in all other stream reaches (see Strauch et al. (2015) for additional detail). In three study reaches (Manoloa, Waikaumalo and Pahoehoe), we supplemented gaps in daily stream flow using a Distributed Hydrology Soil Vegetation Model for the North Hilo coast (DHSVM; Strauch et al., 2016).

Stream flow metrics

We generated nine flow metrics from daily stream flow data describing magnitude, frequency, duration, timing, and rate of change of stream flow for study reaches (Table 2.2). In

addition to representing different aspects of the flow regime, we chose these metrics based on their suggested relevance or observed relationships to stream biology within published literature. Two of the metrics describe stream flow magnitude. Oki et al. (2010) found that the 70th percent exceedance value (Q₇₀) is broadly representative of baseflow conditions in Hawaiian streams, and therefore we included Q_{70} normalized by catchment area (hereafter Q_{70} yield) to characterize potential differences in baseflow across study reaches. April runoff normalized by catchment area (AR yield) quantified stream flow magnitude prior to the sampling season, and coefficient of variation (CV) of daily stream flows characterized flow variability. We represented the frequency of low flows as the total number of events where daily flow fell below 5% of mean annual flow (FL) and differences in the duration of low flow events using the minimum of 7-day mean flow normalized by catchment area (DL yield). We considered high flow periods when daily flows were above 25th percentile exceedance values; the frequency and duration of these events were also included as metrics for analysis. We represented aspects of stream flow timing and rate of change using constancy (CON) and rise rate yield (RR yield), respectively. Constancy is a measure of overall day to day stability in stream flow throughout the year, meaning a stream with seasonal high flows would have a lower constancy than one with numerous but regular high flow events throughout the year (Colwell, 1974; Gordon et al., 2004). We included average rise rate of daily flow normalized by catchment area (RR yield) to represent differences in the relative rate of change in days with increased flow over the previous day.

We calculated stream flow metrics for four time periods: the full period of flow record (2012, 2013 and 2014 water years) and for three seven-month time periods prior to each sampling season (October-April; Table C2.1.). The seven-month time period was chosen for

calculation of flow metrics to allow for a comparative period in which flow data were available across all years leading up to the beginning of the sampling season. We calculated Q_{70} yield and AR yield manually and the other seven flow metrics using the USGS Hydrologic Index Tool (Henriksen et al., 2006; Table 2.2).

Habitat

Stream habitat data sampling

A transect approach was used to collect habitat data from stream reaches during May-August of 2012, 2013, and 2014. Study reach lengths equal to 20 times mean stream width (MSW) at the time of sampling were established to capture a representative sample of habitat in each of the 11 reaches (Kido, 2008; Kido, 2013). Transects lines were established once every MSW over study reaches. Moving upstream, two researchers visually recorded the percent (within $\pm 5\%$) of substrate categories comprising the stream reach including silt, sand, gravel, cobble, boulder and bedrock (following Higashi & Nishimoto, 2007; Table C2.2). Similarly, geomorphic units (riffle, run, pool, cascade) within 1 m of the transect line were also recorded (Higashi & Nishimoto, 2007). Wetted width was measured to the nearest 0.1 m, and maximum water depth along the transect line was measured to the nearest 0.01 m. In 2013 and 2014, we also recorded the total percent ($\pm 5\%$) substrate covered by aquatic moss and filamentous algae within 1 m of the transect line. Values were averaged across transects to assess relative habitat conditions within each reach.

Stream habitat factors

We calculated six habitat factors from sampled habitat data in each reach each year to assess potential changes in habitat which may influence food resources and available habitat for *A. bisulcata*. Average wetted transect area (Knighton, 1998) was calculated by multiplying

transect wetted width by one-half of maximum depth, then averaging these products across transects. Mean substrate size was calculated by multiplying the average percent substrate within a reach by geometric mean of particle size range, with bedrock set to 5656 mm (following Kaufmann & Robison, 1998; Table C2.2). Percent riffles and pools were averaged across all wetted transects within a study reach to capture differences in geomorphic habitat composition. In 2013 and 2014, we averaged percent algae and percent moss cover across transects to assess differences in available food resources including both filamentous algae (Couret, 1976) and FPOM held within moss (Maurer & Brusven, 1983).

A. bisulcata

A. bisulcata sampling

We sampled *Atyoida bisulcata* each year when habitats were sampled, approaching each transect from downstream with a hand seine net (2 mm mesh; 0.91 m wide and 0.45 m deep) and completing a single pass to capture *A. bisulcata* in habitats within 1 m of each transect line. The total numbers of *A. bisulcata* collected from each transect were recorded, and a subsample of all individuals (typically 75-125 individuals) was taken for further analysis. In some instances, transects were excluded from the study if their locations were not accessible (e.g., due to debris) in any sample year. In 2013 and 2014, we also sampled individuals from the upstream plunge pool in reaches with few individuals found within transects. At 2 m intervals around the perimeter of the plunge pool, we seined all *A. bisulcata* within a 1 m² area and a subsample of all captured individuals was considered representative of the population within the stream reach and taken to the lab for further analysis.

Laboratory processing of A. bisulcata

Within 24 hours of collection, we measured individual specimens in the lab. We measured post-orbital carapace (POC) length, the linear distance from the posterior of the ocular cavity to the posterior of the carapace, to the nearest 0.1 mm using an ocular micrometer. Sex was determined based on shape of the endopod of the first pleopod (sinusoidal in males; long and tapering in females) and the presence of the *appendix masculina* on the second pleopod of males (Chace, 1983; Couret, 1976). We recorded small specimens as juveniles if their first pleopod did not show characteristics associated with either sex. In 2013 and 2014, we inspected individuals for brown spot disease, which is an infection of the exoskeleton by chitinoclastic bacteria that is theorized to be more common in *A. bisulcata* living in extreme or degraded environmental conditions (Chan, 1978).

On a subset of measured individuals (typically 75-100) from each subsample, we recorded wet weights for each specimen to the nearest 0.001 g. We dried specimens at 60-105° C for at least 24 hours, reweighed, then combusted them at 500°C in a muffle furnace for at least 2.5 hours to obtain AFDM (Benke et al., 1999). In Kaawalii Stream in 2013, AFDM measurements were not available and were derived from dry weights.

A. bisulcata population characteristics

We calculated four population characteristics for each reach each year. We calculated the first population characteristic, average POC (mm) length, by averaging individual POC length measurements from males within a subsample. Females were excluded in calculation of POC (mm) length due to their low representation in samples and evidence of size stratification by sex. We calculated the second characteristic, the prevalence of brown spot disease, as the percent occurrence of the disease for subsamples with greater than 30 adult males present. Females and

juveniles were excluded from brown spot disease prevalence calculations to avoid disease detection biases resulting from post-egg release molting in females (Chan, 1978; Nishimoto & Kuamo'o, 1996) and high molting rates in juveniles (Couret, 1976). The third population characteristic, average relative mass, was obtained by first generating length-mass relationships for each reach each year using the linear form of the basic length-mass model:

$$\log_{10} \mathbf{M} = \log a + b \log \mathbf{L}$$
 [1]

where M is mass (AFDM; g), L is length (POC length; mm) and *a* and *b* are constants (Benke et al., 1999). Geometric means of *a* and *b* (a_m and b_m , respectively) were calculated from lengthmass regressions from each reach each year (Froese, 2006; Table C2.3). We calculated the relative mass (M_{rm}) of each individual using the formula:

$$M_{\rm rm} = 100 \frac{M}{a_m L^{b_m}}$$
[2]

and average relative mass was then calculated for all males for each reach each year. Froese (2006) suggests that when distinguishing differences in individual condition across multiple sample areas, comparing observed relative mass to predicted relative mass from a mean length-weight relationship is appropriate. Individuals with weights greater than 100% would potentially indicate those in relatively "better" condition than those with weights that fall well under 100%. We excluded females and juveniles from averages of relative mass to avoid biases resulting from differences in body shape (Froese, 2006) and post-egg release declines in relative mass among females. The final population characteristic, average biomass per m² of wetted width (g/m²), was calculated by first finding the proportions of individuals in 0.5 mm POC length-classes in each reach each year. Abundance counts were multiplied by the size-class proportions to estimate the number of individuals within each 0.5 mm size-class at each transect (following Cross et al., 2008). Length-mass regressions were used to predict an average AFDM for each

size-class, which was multiplied by the size-class counts and summed to estimate biomass at each transect. Biomass at each transect was then divided by wetted width and averaged across transects. If an individual transect was dry at the time of sampling, it was excluded from average biomass estimates.

Data analysis

Variation in flow metrics across the study region and relationships to rainfall

We calculated descriptive statistics (average, minimum, maximum, standard deviation, and coefficient of variation) of the nine stream flow metrics across stream reaches for the entire period of record. In addition to descriptive statistics over the entire period of record, means for the seven-month flow period each year were generated along with the coefficient of variation of these means across years to assess relative differences in annual variation of stream flow metrics within the study region. We assessed Pearson's correlations between stream flow metrics and drainage area (as calculated in Tingley, this volume a) to determine if flow metrics co-varied with stream size, and we also examined correlations between mean annual rainfall and the stream flow metrics. Prior to analysis, flow metrics were transformed using natural log (x+1). *Association between habitat factors and flow metrics*

We generated descriptive statistics for the six habitat factors averaged across years for each stream reach. We examined Pearson correlations between the six habitat factors and nine stream flow metrics calculated over the entire period of record.

Association between A. bisulcata population characteristics, flow metrics, and habitat factors

We calculated descriptive statistics each year to assess the range and variation in *A*. *bisulcata* population characteristics across the study reaches and across years. When then used a multi-step approach to assess strength and consistency of relationships between *A*. *bisulcata*

population characteristics and stream flow metrics across years. First, because we were interested in the effects of differences in rainfall on *A. bisulcata* operating through the flow regime, we selected stream flow metrics that had been shown to have strong (r > |0.60|) and significant (p < 0.05) correlations with mean annual rainfall for use in the analysis with population characteristics. In some cases, if selected stream flow metrics were highly redundant (r > |0.9|), we included a single flow metric. Then, we calculated Pearson's correlation coefficients between the selected stream flow metrics summarized over each seven-month flow period and the *A. bisulcata* population characteristics independently for each year that detailed biological data were collected (2012, 2013, 2014).

Results

Variation in flow metrics across the study region and relationships with rainfall

Most stream flow metrics varied across the study region and some had high measures of variability (as indicated by coefficients of variation greater than 100) across study years (Table 2.3). Q_{70} yield and minimum 7-day mean flow yield had the most variability (coefficient of variations of 132.2 and 175.2, respectively) across study reaches over the entire period, and both metrics had minimum values below measurable levels. Coefficients of variation of daily flows were above 100% in all sites with a mean of 472.8, suggesting that stream organisms often experience high and in some cases extreme variability in stream flows. The frequency of low flow events and rise rate yield were also relatively variable across sites, with coefficients of variation of 66.9 and 75.8, respectively. The duration of high flow events was relatively short across all stream reaches, ranging from 2.1 to 4.2 days with a mean of 3.4. For most stream flow metrics, mean values of the 7-month period prior to each sampling season were similar across years, but coefficients of variation were highest for April runoff yield (112.1) and Q_{70} yield

(50.3). Mean of Q_{70} yield summarized over the 7-month period across all sites in 2012 was nearly double that of the 2013 value (13.3 vs. 7.8 L/s/km², respectively) and one third of the mean in 2014 (4.7 L/s/km²), suggesting that inter-annual variation in total rainfall likely resulted in substantial differences in baseflow over our study years. Flow conditions prior to the sampling season differed greatly across years; April runoff was approximately 25 times higher in 2014 than 2013 (23.6 vs 588.9 ML/km²).

Mean annual rainfall had strong and significant correlations with six of the nine stream flow metrics calculated over the entire period of record, indicating that rainfall along the North Hilo Coast has strong controls on stream flow magnitude and variability (Table 2.4). Of the nine stream flow metrics, Q_{70} yield had the strongest positive correlation with mean annual rainfall (r = 0.91). We selected five stream flow metrics with strong and significant correlations with mean annual rainfall for further comparison with population characteristics. We excluded minimum 7day mean flow yield given its redundancy (r \ge 0.9) with multiple metrics and its limited ecological interpretability when compared to Q_{70} yield. April runoff yield was included despite its redundancy with the frequency of high flow events (r = 0.94), given that it is a short-term representation of flow conditions prior to the sampling season that has greater year-to-year variability than other stream flow metrics.

Variation in habitat factors across the study region and relationships with rainfall

Similar to stream flow metrics, stream habitat factors also varied across the study reaches (Table 2.5). Mean wetted area was 2.1 m^2 , with values ranging from 0.1 to 9.1 m^2 . The minimum substrate size across stream reaches was 1071 mm and the mean was 2353 mm, indicating that study reaches were predominately composed of large substrate (i.e., bedrock, boulders). Reaches ranged from those predominantly composed of pools (90.7%) to those in

which pools were rare (0.8%). Riffles were less common across sites, with a maximum of 29.5%. Mean percent moss and percent algae cover were both close to 10% (9.9 and 9.6%, respectively).

Percent pool habitat, riffle habitat, moss cover, and algal cover all had strong and significant correlations with at least one of the six stream flow metrics correlated with mean annual rainfall (Table 2.6). This suggests that rainfall likely has indirect relationships with other characteristics of habitat through controls on the stream flow regime. Percent pools and riffles had directionally opposite correlations with all stream flow metrics. For instance, pools were negatively correlated with metrics of flow magnitude, the frequency of high flow events and minimum 7-day mean flow yield, while riffles were positively correlated with these metrics. Both percent pools and percent riffles and were both most strongly correlated with Q_{70} yield (-0.77 and 0.91, respectively). While multiple stream flow metrics were correlated with percent moss cover, it was most strongly correlated with frequency of low-flow events (r = -0.90). The frequency of low flow events was also the only stream flow metric with strong and significant correlations with percent algae (r = 0.67).

Associations among *A. bisulcata* population characteristics, flow metrics, and habitat factors

All four population characteristics showed a range in values across study reaches, but descriptive statistics were similar across years (Table 2.7). Average and maximum POC length was relatively constant across years and range in POC length across sites was less than 2.5 mm in all years. The range in average relative mass across sites was similar across years, with ranges between 26% and 32% in all years of the study. The mean of average relative mass across sites was below 100% in 2012 (97.9%) and 2013 (96.2%), but above 100% in 2014 (108.0%). The

minimum value of percent relative mass for stream reaches was also much higher in 2014 than 2013 and 2012 (95.2 vs 84.1 and 80.3%, respectively), suggesting that overall individuals were in better condition across sites in 2014. Brown spot disease was never found on more than 20.5% of males within a reach in a given year, and the disease was not observed in at least one stream in both years it was monitored. Average biomass had minimum values of zero in all years and mean values ranging from 0.24 to 0.33 g/m^2 . In two streams in 2012 (Pahale and Manowaiopae) and one stream in 2014 (Kaawalii), estimates of relative mass, average POC length and the prevalence of brown spot disease were not calculated due a lack of males within samples (Table C2.5).

All population characteristics had strong correlations with at least one of the five stream flow metrics considered in at least two years, suggesting that multiple aspects of stream flow may have effects on populations of *A. bisulcata* (Table 2.8). Average POC length had a strong positive correlation with median baseflow yield in all three years (r = 0.82, 0.87, and 0.80; Figure 2.2). Average relative mass had a strong positive correlation with median baseflow yield in 2012 and 2013 (r = 0.72 and 0.78) but not in 2014 (Figure 2.3). The prevalence of brown spot disease had strong positive correlations with the coefficient of variation in daily flows in both 2013 and 2014 (r = 0.62 and 0.77, respectively; Figure 2.4). Biomass had strong positive correlated with median baseflow yield (r = 0.75, 0.82, and 0.87; Figure 2.4) and the frequency of low flow events (r = -0.79, -0.83, and -0.77). Associations between population characteristics of *A. bisulcata* and habitat factors largely reflect changes in habitat associated with differences in the stream flow regime (Table 2.9) which suggests that changes in the habitat factors and population characteristics occur with changes to the stream flow regime.

Discussion

Our results highlight the potential effects of climate change on tropical island streams, which can be used to inform the proactive conservation of stream species as climate change progresses. Multiple aspects of the stream flow regimes across our study reaches were sensitive to mean annual rainfall, and several habitat factors also varied with differences in the rainfallsensitive flow metrics. Relationships between rainfall-sensitive flow metrics and population characteristics of A. bisulcata (Figure 2.2, Figure 2.3, and Figure 2.4) suggests that populations across the North Hilo coast are sensitive to changes in the flow regime controlled by rainfall. In streams with lower baseflows at the drier end of the rainfall gradient, we observed populations of A. bisulcata composed of smaller individuals in poorer condition, which, along with an increase in the frequency of low flows, contributed to lower total biomass within streams. Higher flow variability in drier streams was also associated with increased prevalence of brown spot disease, suggesting that populations exposed to more extreme flow conditions are more prone to infection. Overall, our study offers important insights into influences of stream flow characteristics on populations of A. bisulcata and demonstrates the value of using population characteristics to study effects of stream flow on tropical stream organisms.

Variation in flow metrics and their relationship to rainfall

Our results indicate strong relationships between magnitude of annual rainfall and multiple metrics of stream flow, emphasizing that annual rainfall is the dominant factor influencing stream flow magnitude, variability, and duration and frequency of ecologically important flow events in our study streams. While these relationships have been described previously and have been attributed to relatively small drainage areas, high slopes, and limited groundwater inputs of these streams (Strauch et al., 2015), our results underscore the strength of

these relationships. The consistency of values of Q_{70} yield below measurable levels in several drier reaches across years and the high inter-annual variability in average Q_{70} yield across reaches shows the sensitivity of baseflow within these streams to differences in mean annual rainfall. This supports current understanding that baseflows in Hawaiian streams are extremely sensitive to changes in rainfall (Bassiouni and Oki, 2013; Frazier and Giambelluca, 2016), which in turn suggests these systems are highly vulnerable to projected declines in rainfall associated with climate change (Timm et al, 2015).

Variation in habitat factors across the study region and relationships with rainfall

Our results also show that the stream flow regime influences the type of habitat and availability of moss and filamentous algae within reaches, outcomes that may have implications for habitat and food availability for *A. bisulcata*. This is not surprising, as declining baseflow results in changes to stream habitat types and reduces hydraulic habitat complexity (Rolls et al., 2012). In headwater streams of West Virginia, abnormally low baseflow due to drought temporarily reduced riffle habitat within seven stream reaches by half but had little to no effect on total amount of pool habitat (Hakala & Hartman, 2004). In our study region, this homogenization of habitat types is apparent in streams with lower baseflow at the drier end of the gradient, with pools more prevalent in drier reaches and riffles largely absent. These differences in habitat in drier reaches may have negative consequences for *A. bisulcata*, given that the species may preferentially select higher velocity habitats (Couret, 1976; Brasher et al., 1997).

Greater aquatic moss cover within a reach is often associated with more stable environments and high baseflow (Bowden, 1999), and strong correlations between stream flow magnitude, frequency of low flow events, and flow variability with percent moss cover in our

study reaches supports this understanding. While A. bisulcata is not suspected to feed on aquatic moss (Riney, 2015), it can potentially act as high-quality habitat for macroinvertebrate species that traps FPOM and contains high levels of epiphytic microalgae (Maurer & Brusven, 1983; Brusven et al., 1990), increasing foraging opportunities indirectly for grazers (Bowden, 1999). Percent filamentous algae cover is only significantly correlated with increasing frequency of low flow events, but similar insignificant correlations with Q_{70} yield and the minimum 7-day mean flow further indicate that filamentous algae are more abundant in streams with lower baseflow and longer and more frequent low flow periods. Streams with low baseflow and long low-flow periods have fewer high flow events, higher temperatures, and more light associated with shallower habitat, all which can encourage the growth of filamentous algae (Cummins, 1974). While not a primary component of their diet, a recent stable isotope analysis indicated that filamentous algae may provide a secondary food source for A. bisulcata (Riney, 2015). While this may suggest that A. bisulcata have ample food resources in streams with lower rainfall, Riney (2015) also found that the percent contribution of algae to their diets did not increase even in streams with very low baseflow, suggesting that reductions in rainfall with climate change will not result in increased food availability.

Association between A. bisulcata population characteristics and flow metrics

Baseflow and frequency of low flows

Across the North Hilo Coast of Hawaii Island, stream reaches with lower baseflows support populations of *A. bisulcata* composed of smaller individuals in relatively poorer condition than populations in streams with higher baseflows. In addition, streams with the highest baseflow had the highest average biomass, while those with the lowest baseflow and the highest frequency of low flows had the lowest average biomass. These results suggest that the

stream flow regime influences populations of *A. bisulcata* both directly through controls on available habitat and potentially through indirect controls on food availability and temperature.

Temporary habitat desiccation

Very low baseflow and frequent low flows can lead to temporary habitat desiccation, resulting in substantial loss of organism biomass within streams (Rolls et al., 2012). We observed very low biomass estimates in reaches with higher frequencies of low flows and lower baseflow, suggesting that temporary reductions in habitat in these reaches may have been responsible. In all years of this study, habitat surveys showed that reaches with low mean annual rainfall were comprised mostly of isolated pools throughout the channel. However, *A. bisulcata* were rarely captured within these habitats and instead were found in upstream plunge pools (depth >2 m). Use of plunge pool habitats by *A. bisulcata* in rivers with low baseflow supports the understanding that these habitats, while comprising a low proportion of the stream under normal flows, are important to the persistence of populations during periods of reduced flow (McRae, 2007). Our results also indicate that reaches with larger upstream catchments may provide refugia for *A. bisulcata* during times of low flow, as reaches with large upstream catchments (>30 km²) with low baseflow (Waikaumalo and Umauma) had moderate measures of biomass in all years (Figure 2.5; Table C2.4).

Food availability

In our study, limited food availability in streams with lower baseflow likely resulted in lower average relative mass in 2012 and 2013 and may be responsible for observed differences in average POC length. *A. bisulcata* are opportunistic filterers/grazers assumed to filter FPOM in high velocity areas of the reach as well as graze on benthic resources (Couret, 1976). This suggests that declines in overall foraging space and habitats for filter feeders associated with

lower baseflow may limit food availability. Riney (2015) found through stable isotope analysis that biofilm was a predominant component of adult *A. bisulcata* diets in our study region, even in reaches with lower stream flow and limited concentrations of biofilm. The diet of a similar filterer/grazer atyid species in Australian streams, *Paratya australiensis*, consists largely of cyanobacteria selectively grazed from biofilm (Burns & Walker, 2000). Given that biofilm shifts from predominantly autotrophic to heterotrophic communities as baseflow declines (Timoner et al., 2012), a reduction in both the quality and quantity of food may occur with declining stream flow, with likely negative effects on both the growth and condition of *A. bisulcata*.

The lack of a relationship between Q_{70} yield and average relative mass in 2014 may have resulted from seasonal anomalies in baseflow. April runoff yield was substantially higher in 2014 than 2013 and 2012 across our stream reaches, suggesting that average relative mass may be sensitive to temporary increases in food availability resulting from higher baseflow. Many studies have documented variability in organism condition with short-term or seasonal changes in food availability (e.g., Hakala & Hartman, 2004; Currinder et al., 2014; Miller et al., 2015), which may indicate differences in individual growth rates (Bentley & Schindler, 2013).

Stream temperature

In addition to limited food availability, higher stream temperatures may contribute to smaller *A. bisulcata* in streams with lower baseflow. Increases in rearing temperature of ectotherms results in lower maximum adult size (as reviewed by Atkinson et al., 1994). Across several of our study reaches, Strauch et al. (2017) demonstrated that mean dry season water temperature increased as baseflow decreased. Given that we observed declines in adult POC length with declines in steam baseflow, it is possible that higher average stream temperature

results in lower maximum adult size. This relationship requires further study, as climate change will result in increased air temperatures and in turn alter stream temperatures.

Flow variability and brown spot disease

Increases in the coefficient of variation in daily flows associated with declines in mean annual rainfall may result in higher rates of carapace infection by chitinoclastic bacteria in populations of *A. bisulcata*. While the exact mechanism causing increased prevalence of brown spot disease in *A. bisulcata* is not clear, previous research suggests that carapace surface abrasions increase susceptibility to infection (Chan, 1978). Abrasive forces acting upon macroinvertebrates in streams are increased during periods of increased suspended sediment loads (Jones et al., 2012). Preliminary analysis of measures of turbidity from 2012-2014 in our study area does show higher sediment loads during flood events in streams receiving less annual precipitation, but these data are only available from three reaches (unpublished data). Further study of differences in sediment loading during high flow events may identify additional factors influencing prevalence of brown spot disease.

Implications for assessing climate change effects and prioritizing conservation action

Our results demonstrate the value of considering population characteristics when assessing effects of climate change through changes in flow regimes on stream organisms. Understanding how climate-driven changes in flow may affect population characteristics such as individual size, condition and susceptibility to disease is essential when considering effects of climate change, as these measures may reflect the mechanisms which drive species loss. This approach holds promise for the proactive conservation of other organisms as well, as changes in the flow regime are likely to occur in many systems with future changes in climate. In addition, Hawaiian streams support other endemic fish, shrimp and snails of conservation concern.

Differences in stream flow likely influence these species, and further research that identifies relationships between population characteristics of these organisms and the stream flow regime can improve proactive conservation decision-making in Hawaii.

Current climate projections indicate that changes in total annual rainfall will vary regionally across the five main Hawaiian Islands in the coming century, with rainfall increasing in some areas and decreasing in others (Timm et al., 2015). Our results suggest that in areas where rainfall declines, baseflows may decrease but flow variability may increase. This will likely have negative effects on stream organisms, as evidenced in our study by declines in A. *bisulcata* individual size and relative mass with reductions in baseflow as well as increases in disease prevalence with higher flow variability. This information suggests that proactive conservation strategies that consider prioritization in the context of climate change are necessary, but specific actions may differ depending on projected changes in rainfall and current habitat condition. For instance, in areas that currently support populations of native stream organisms but are likely to experience declines in rainfall, it is important to maintain and if possible increase stream baseflow by minimizing and removing water diversions. In areas not likely to experience declines in rainfall, conservation strategies may include the protection of streams that currently have high baseflow and minimal anthropogenic disturbance in the catchment, given these areas will likely provide the best habitat for stream species in the future (Tingley this volume c). In addition, areas that are moderately disturbed but are not projected to decline in annual rainfall may be optimal for restoration projects that improve habitat and increase baseflow.

APPENDICES

APPENDIX 2.A

Tables

	Network	Mean annual	
	catchment	rainfall	Elevation
Stream	area (km ²)	(mm/year)	(m)
Honolii	30.4	5252	470
Pahoehoe	1.3	5487	430
Kolekole	17.2	5982	500
Kapue	20.7	5257	460
Umauma	46.0	4441	490
Waikaumalo	36.0	3410	450
Manoloa	2.6	4759	420
Makahiloa	9.6	4263	400
Pahale	10.1	3676	510
Manowaiopae	3.8	4271	470
Kaawalii	33.1	2724	475

Table 2.1. Network catchment area, mean annual rainfall in catchments, and elevation of the eleven study reaches. Streams are listed geographically from south to north across the study area (Figure 2.1).

Aspect of				
flow regime	Flow metric	Metric name	Units	Description
Magnitude				
C	Q ₇₀ yield	Q ₇₀ yield	L/s/km ²	Seventieth percentile exceedance
	AR yield	April runoff yield	ML/km ²	Total April runoff in million liters divided by catchment area
	CV*	Coefficient of variation	-	Standard deviation of daily flow divided by the mean
Frequency				
1	FL*	Low flow frequency	Count	Total number of low flow events below 5% of mean annual daily flow
	FH*	High flow frequency	Count	Total number of flow events in a year greater than the 25 th percentile exceedance
Duration	DL yield*	Minimum 7-day mean flow	L/s/km ²	Minimum of 7-day mean flow divided by catchment area
T	DH*	Duration of high flow	Days	Duration of high flow events as represented by FH
Timing	CON*	Constancy	-	Stability in day to day stream flows over the study period
Rate of chan	ge			
	RR yield*	Rise rate yield	L/s/km ²	Average rise rate of days with increased flow over previous day divided by catchment area

 Table 2.2. Stream flow metrics generated for each stream reach using daily flow data.

 Aspect of

*Metrics calculated using the USGS Hydrologic Index Tool (HIT; Henriksen et al., 2006) with descriptions modified from Olden & Poff (2003).

· ununon or i	nose mean varaes.										
Aspect of											CV of
flow	Flow					Std.		2012	2013	2014	yearly
regime	metric	Units	Mean	Min	Max	deviatio	on CV	mean	mean	mean	means
Magnitude											
	Q ₇₀ yield	$L/s/km^2$	8.2	0.0	34.5	10.9	132.2	13.3	7.8	4.7	50.3
	April runoff yield	ML/km^2	261.4	16.3	497.7	135.4	55.6	172.0	23.6	588.9	112.1
	Coefficient of variation	-	472.8	178.3	840.1	214.1	45.2	198.8	340.7	425.2	35.6
Frequency											
	Frequency of low flows	Count	13.9	0.7	23.3	9.3	66.9	7.8	7.5	8.6	7.6
	Frequency of high flows	Count	22.8	10.3	27.7	5.3	23.3	15.6	11.7	13.4	14.2
Duration											
	Minimum 7-day mean flow	L/s/km ²	3.8	0.0	22.2	6.7	175.2	5.2	4.5	3.3	22.5
	Duration of high flows	Days	3.4	2.2	4.2	0.5	16.3	3.9	4.7	4.4	9.7
Timing											
	Constancy	-	0.47	0.32	0.61	0.11	22.6	0.45	0.48	0.46	3.3
Rate of char	nge	_									
	Rise rate yield	L/s/km ²	215.8	10.3	565.4	163.7	75.8	282.3	129.2	301.5	39.7

Table 2.3. Descriptive statistics for selected stream flow metrics across the 11 study reaches for the entire period of record. Also shown are the mean values of each stream flow metric for each 7-month period prior to the sampling season and the coefficient of variation of these mean values.

	ΜΑΡ	D۸	Q ₇₀	CV	AR	БI	БП	DL	лц	CON	RR
	MAK	DA	yleid	CV	yleid	ГL	ГП	yleid	ЪΠ	CON	yleid
MAR	1.00	-0.31	0.91	-0.72	0.62	-0.68	0.64	0.82	0.19	0.31	0.32
DA		1.00	-0.13	0.15	-0.14	0.12	-0.05	-0.17	0.12	0.24	-0.10
Q70 yield			1.00	-0.82	0.50	-0.78	0.46	0.95	0.30	0.53	0.12
CV				1.00	-0.27	0.83	-0.18	-0.89	0.15	-0.61	0.11
AR yield					1.00	-0.03	0.94	0.33	0.02	-0.22	0.90
FL						1.00	-0.05	-0.90	-0.17	-0.64	0.34
FH							1.00	0.27	0.14	-0.18	0.87
DL yield								1.00	0.26	0.60	-0.09
DH									1.00	0.10	-0.08
CON										1.00	-0.56
RR yield											1.00

Table 2.4. Pearson's correlation coefficients describing relationships between mean annual rainfall (MAR), drainage area (DA) and stream flow metrics. Correlation coefficients greater than an absolute value of 0.6 and significant (α =0.05) are shown in bold.
Habitat characteristic	Units	Mean	Minimum	Maximum	Std. deviation
Wetted area	m^2	2.1	0.1	9.1	2.66
Mean substrate size	mm	2353	1071	4356	1120.3
Pool habitat	%	35.6	0.8	90.7	31.98
Riffle habitat	%	12.8	0.0	29.5	10.99
Moss cover	%	9.9	0.0	33.6	14.39
Algal cover	%	9.6	0.3	20.8	7.08

Table 2.5. Descriptive statistics for habitat factors across study reaches averaged across years.

Aspect of			Mean				
flow		Wetted	substrate	Pool	Riffle	Moss	Algae
regime	Metric	area	size	habitat	habitat	cover	cover
Magnitude							
	Q ₇₀ yield	0.57	-0.40	-0.77	0.91	0.76	-0.52
	April runoff yield	0.27	-0.16	-0.76	0.49	0.24	-0.06
	Coefficient of variation	-0.51	0.34	0.46	-0.73	-0.71	0.44
Frequency							
	Frequency of low flows	-0.59	0.41	0.40	-0.68	-0.90	0.67
	Frequency of high flows	0.44	-0.16	-0.72	0.46	0.23	-0.13
Duration							
	Minimum 7-day mean flow	0.52	-0.37	-0.65	0.86	0.82	-0.57
	Duration of high flows	0.25	0.00	-0.34	0.26	0.15	-0.40
Timing							
U	Constancy	0.53	-0.06	-0.14	0.43	0.36	-0.30
Rate of cha	nge						
	Rise rate yield	0.06	-0.04	-0.50	0.13	-0.06	0.16

Table 2.6. Pearson's correlation coefficients between stream flow metrics and habitat factors. Correlation coefficients greater than an absolute value of 0.60 and significant (α =0.05) are shown in bold.

Population				
characteristic	Statistic	2012	2013	2014
POC length (n	nm)			
	Mean	6.1	6.1	6.0
	Minimum	5.3	5.2	4.8
	Maximum	7.3	7.3	7.1
	Range	2.0	2.1	2.3
	Std. Deviation	0.78	0.76	0.77
Relative mass	(%)			
	Mean	97.9	96.2	108.0
	Minimum	84.1	80.3	95.2
	Maximum	110.2	112.1	120.1
	Range	26.1	31.8	24.9
	Std. Deviation	8.21	9.78	6.74
Brown spot (%	b)			
	Mean		6.7	6.5
	Minimum		0.0	0.0
	Maximum		20.5	13.5
	Range		20.5	13.5
	Std. Deviation		7.13	5.23
Biomass (g/m ²	²)			
	Mean	0.33	0.27	0.24
	Minimum	0.00	0.00	0.00
	Maximum	0.82	0.80	0.67
	Range	0.82	0.80	0.67
	Std. Deviation	0.300	0.290	0.240

Table 2.7. Descriptive statistics for *A. bisulcata* population characteristics across sites for each sample year.

Population		2012	2012	2014
characteristic	Flow metric	2012	2013	2014
POC length				
	Q70 yield	0.82	0.87	0.80
	Coefficient of variation	-0.60	-0.88	-0.47
	April runoff yield	0.54	0.83	0.68
	Frequency of low flows	-0.34	-0.73	-0.55
	Frequency of high flows	-0.19	-0.24	0.33
Relative mass				
	Q70 yield	0.72	0.78	0.36
	Coefficient of variation	-0.74	-0.59	0.11
	April runoff yield	0.46	0.78	0.51
	Frequency of low flows	-0.58	-0.49	-0.22
	Frequency of high flows	-0.59	-0.59	-0.39
Biomass				
	Q70 yield	0.75	0.82	0.87
	Coefficient of variation	-0.76	-0.85	-0.45
	April runoff yield	0.16	0.78	0.23
	Frequency of low flows	-0.79	-0.83	-0.77
	Frequency of high flows	-0.55	-0.35	-0.20
Brown spot				
	Q70 yield	•	-0.56	-0.63
	Coefficient of variation	•	0.62	0.77
	April runoff yield	•	-0.53	0.51
	Frequency of low flows	•	0.36	0.63
	Frequency of high flows	•	0.55	0.55

Table 2.8. Pearson's correlation coefficients between *A. bisulcata* population characteristics and stream flow metrics. Correlation coefficients greater than 0.6 and statistically significant (α =0.05) are shown in bold.

Population				
characteristic	Habitat factor	2012	2013	2014
POC length				
	Wetted area	0.48	0.46	0.48
	Mean substrate size	-0.59	-0.38	-0.29
	Pool habitat	-0.24	-0.76	-0.72
	Riffle habitat	0.58	0.77	0.84
	Moss cover		0.75	0.79
	Algal cover		-0.49	-0.49
Relative mass				
	Wetted area	-0.08	0.38	-0.26
	Mean substrate size	-0.53	-0.27	-0.01
	Pool habitat	-0.64	-0.91	-0.49
	Riffle habitat	0.53	0.68	0.41
	Moss cover		0.65	0.31
	Algal cover		-0.52	-0.10
Biomass				
	Wetted area	0.57	0.67	0.63
	Mean substrate size	-0.04	-0.18	-0.21
	Pool habitat	-0.53	-0.64	-0.79
	Riffle habitat	0.30	0.58	0.62
	Moss cover		0.80	0.86
	Algal cover		-0.62	-0.72
Brown spot				
	Wetted area		-0.40	-0.52
	Mean substrate size		0.13	0.36
	Pool habitat		0.52	0.20
	Riffle habitat		-0.71	-0.45
	Moss cover		-0.25	-0.55
	Algal cover		-0.08	0.66

Table 2.9. Pearson's correlation coefficients between *A. bisulcata* population characteristics and habitat factors. Correlation coefficients greater than 0.6 and statistically significant (α =0.05) are shown in bold.

APPENDIX 2.B

Figures



Figure 2.1. North Hilo coast of Hawaii Island and locations of study reaches along a gradient in mean annual rainfall.



Figure 2.2. Average post orbital carapace length (mm) of males versus the natural log (x+1) of Q_{70} yield. Panels show 2012 (A), 2013 (B) and 2014 (D) data.



Figure 2.3. Average relative mass of individuals collected during each sampling event versus the natural log (x+1) of Q_{70} yield. Significant correations are denoted by a solid (vs. dashed) trend line. Panels show 2012 (A), 2013 (B) and 2014 (D) data.



Figure 2.4. The percent of male *A. bisulcata* with brown spot disease versus the natural log (x+1) transformed coefficient of variation in daily flows (CV). Panels show 2012 (A) and 2013 (B) data.



Figure 2.5. Average biomass (g/m^2) of *A. bisulcata* versus the natural log (x+1) Q₇₀ yield. Panels show 2012 (A), 2013 (B) and 2014 (D) data.

APPENDIX 2.C

Supplemental tables

	Time	Q ₇₀		AR			DL			RR
Stream	period	yield	CV	yield	FL	FH	yield	DH	CON	yield
Honolii										
	Full	10.00	a 40.00	0.50.01	0.67		0.40	. ==	0.51	110 50
	record	19.30	240.88	253.21	0.67	25.67	8.49	3.77	0.61	113.50
	2012	27.20	198.83	228.74	1.00	16.00	7.86	3.31	0.56	169.39
	2013	18.09	223.64	58.43	0.00	8.00	11.71	6.63	0.68	91.05
	2014	11.45	262.69	472.46	0.00	12.00	7.82	4.42	0.57	121.75
Pahoeho	be E ll									
	Full	24 52	170.22	262 75	0.67	10.00	22.25	2 50	0.52	80.00
		54.55 (2.90	1/8.33	202.75	0.07	19.00	22.25	3.50	0.52	80.00
	2012	63.80	120.21	2/8.68	0.00	0.00	34.90	8.07	0.52	93.15
	2013	36.58	1/9./1	88.10	0.00	14.00	23.80	3.79	0.59	/5.65
T Z 1 1 1	2014	21.44	285.74	421.46	0.00	7.00	16.55	7.57	0.53	99.18
Kolekol	e Evil									
	Full record	14.01	274 30	283 25	1.00	27 67	6.02	3 10	0.54	150.45
	2012	20.20	274.50	265.25	5.00	18.00	6.51	2 94	0.54	218.96
	2012	13.00	220.12	238.01 40.31	0.00	0.00	6.86	2.94 5.80	0.55	126.00
	2013	7.67	202.27	40.31 551 44	0.00	9.00	5.00	2.52	0.52	120.09
Kapua	2014	7.07	294.33	551.44	0.00	15.00	5.90	5.55	0.55	165.07
Kapue	Full									
	record	10.99	304.93	418.80	13.33	26.67	2.54	3.47	0.51	239.97
	2012	17.90	224.11	345.32	5.00	17.00	2.84	3.12	0.48	360.59
	2013	9.41	270.42	40.44	11.00	11.00	4.19	4.82	0.56	185.62
	2014	5.28	326.53	870.63	13.00	16.00	2.15	3.31	0.51	273.38
Umaum	a									
	Full									
	record	4.85	455.47	515.32	23.33	26.67	1.12	3.08	0.46	454.56
	2012	5.40	371.68	179.20	11.00	19.00	0.96	2.79	0.43	385.51
	2013	2.58	372.88	11.71	13.00	12.00	0.87	4.42	0.53	229.55
	2014	1.24	416.68	764.92	10.00	16.00	0.53	3.31	0.43	406.46
Waikau	malo									
	Full									
	record	0.18	840.13	160.97	22.33	22.00	0.04	4.24	0.35	166.73
	2012	1.70	164.25	7.66	0.00	11.00	0.92	4.82	0.54	3.41
	2013	0.14	435.65	0.64	12.00	11.00	0.08	4.82	0.36	50.46
	2014	0.10	806.19	474.62	13.00	13.00	0.07	4.08	0.40	354.75

Table C2.1. Stream flow metric values for each stream over the entire period of record and each 7-month flow period (October to May) of each year (2012, 2013 and 2014)

Table C2.1. (cont'd)

	Time	Q ₇₀		AR			DL			RR
Stream	period	yield	CV	yield	FL	FH	yield	DH	CON	Yield
Manolo	a									
	Full									
	record	3.90	611.42	290.87	16.00	25.33	1.58	3.93	0.51	188.74
	2012	5.30	136.30	21.41	0.00	10.00	2.76	5.30	0.48	6.15
	2013	3.54	434.65	14.30	8.00	16.00	1.40	3.31	0.45	121.48
	2014	3.25	644.87	836.90	18.00	19.00	2.39	2.79	0.56	652.37
Makahil	loa									
	Full									
	record	2.17	710.15	497.68	22.67	27.33	0.13	3.30	0.32	565.44
	2012	3.90	760.32	228.26	18.00	19.00	0.01	2.79	0.33	1103.13
	2013	2.32	385.54	3.87	12.00	13.00	0.00	4.08	0.32	323.59
	2014	1.01	453.01	1260.90	9.00	14.00	0.04	3.64	0.27	496.79
Pahale										
	Full		• • • • •	•=• • • •		•• • • •			0.40	• • • • •
	record	0.00	388.68	278.81	22.33	22.00	0.00	2.15	0.40	269.65
	2012	0.00	275.64	181.28	15.00	18.00	0.00	2.94	0.28	289.79
	2013	0.00	378.24	0.00	14.00	12.00	0.00	4.42	0.47	182.11
	2014	0.00	364.24	655.13	13.00	16.00	0.00	3.31	0.43	630.64
Manowa	aiopae Full									
	record	0.52	618.93	95.12	19.00	18.00	0.01	3.25	0.32	134.69
	2012	0.90	535.26	162.22	22.00	22.00	0.04	2.41	0.26	457.82
	2013	0.41	389.39	1.28	7.00	10.00	0.00	5.30	0.33	28.55
	2014	0.57	395.58	121.87	13.00	13.00	0.29	4.08	0.36	82.84
Kaawali	ii									
	Full									
	record	0.00	578.11	16.33	11.33	10.33	0.00	3.10	0.60	10.28
	2012	0.00	543.59	1.43	9.00	15.00	0.00	3.40	0.66	17.36
	2013	0.00	415.56	0.05	5.00	13.00	0.00	4.00	0.56	7.18
	2014	0.00	427.38	47.50	6.00	6.00	0.00	8.83	0.47	15.03

	Particle diameter	Geometric mean
Size category	range (mm)	(mm)
Bedrock	4000.00 - 8000.00	5656.854
Boulder	256.00 - 4000.00	1011.929
Cobble	64.00 - 256.00	128.00
Gravel	2.00 - 64.00	11.314
Sand	0.06 - 2.00	0.256
Silt	0.01 - 0.06	0.024

Table C2.2. Substrate size categories and references following Higashi & Nishimoto (2007) used to estimate percent substrate composition and mean substrate size in stream reaches.

Stream	Year	a'	В	R^2
Honolii	2012	$\textbf{-3.59} \pm 0.083$	3.03 ± 0.099	0.94
	2013	-3.75 ± 0.078	3.26 ± 0.093	0.94
	2014	$\textbf{-3.37} \pm 0.087$	2.80 ± 0.104	0.89
Kaawalii	2012*	-3.63 ± 0.234	3.02 ± 0.305	0.85
	2013*	-3.48 ± 0.178	2.84 ± 0.236	0.91
	2014*	-3.52 ± 0.115	2.83 ± 0.221	0.65
Kapue	2012	-3.68 ± 0.095	3.18 ± 0.114	0.92
	2013	$\textbf{-3.77} \pm 0.091$	3.31 ± 0.107	0.93
	2014	-3.46 ± 0.083	2.97 ± 0.100	0.91
Kolekole	2012	-3.50 ± 0.109	2.99 ± 0.125	0.90
	2013	-3.34 ± 0.124	2.83 ± 0.139	0.86
	2014	-3.51 ± 0.090	3.01 ± 0.104	0.90
Makahiloa	2012*	-3.98 ± 0.129	3.61 ± 0.185	0.95
	2013*	-3.36 ± 0.122	2.73 ± 0.175	0.76
	2014*	-2.98 ± 0.135	2.27 ± 0.191	0.61
Manoloa	2012	-3.81 ± 0.080	3.39 ± 0.097	0.95
	2013	-3.54 ± 0.081	3.00 ± 0.101	0.93
	2014	$\textbf{-3.33} \pm 0.088$	2.78 ± 0.112	0.86
Manowaiopae	2012*	-3.93 ± 0.222	3.28 ± 0.272	0.86
	2013	-3.76 ± 0.079	3.17 ± 0.107	0.92
Pahale	2014	-3.80 ± 0.092	3.34 ± 0.134	0.87
	2013	-3.48 ± 0.164	2.90 ± 0.207	0.87
	2014	-3.68 ± 0.165	3.24 ± 0.213	0.93
Pahoehoe	2012	-3.61 ± 0.113	3.15 ± 0.134	0.90
	2013	-3.47 ± 0.132	2.95 ± 0.152	0.84
	2014	-3.14 ± 0.084	2.63 ± 0.098	0.88
Umauma	2012	-3.93 ± 0.063	3.47 ± 0.085	0.96
	2013	-3.71 ± 0.101	3.19 ± 0.127	0.90
	2014	-3.55 ± 0.060	3.03 ± 0.077	0.94
Waikaumalo	2012	-3.75 ± 0.076	3.25 ± 0.101	0.94
	2013	-3.66 ± 0.076	3.15 ± 0.099	0.93
	2014	-3.65 ± 0.057	3.21 ± 0.077	0.95
Geometric mean		-3.57	3.08	

Table C2.3. Length-mass regression coefficients for *A. bisulcata* in each reach each year. Asterisks indicate regressions not used to calculate geometric mean coefficient values due to a dominance by juveniles, limited sample size (n<30) or $R^2 < 0.8$.

					Mean		
			Pool	Riffle	substrate	Algae	Moss
Year	Stream	Area	habitat	habitat	size	cover	cover
2012							
	Honolii	9.97	31	16	1321.70		
	Pahoehoe	0.73	1	26	1730.94		
	Kolekole	4.73	6	31	1902.42		
	Kapue	4.41	7	14	1830.22		
	Umauma	3.18	7	7	4103.02		
	Waikaumalo	1.46	0	2	4643.37		
	Manoloa	0.72	17	6	995.48		
	Makahiloa	1.91	5	28	1855.32		
	Pahale	0.67	46	1	1910.30		
	Manowaiopae	0.14	88	0	1042.86		
	Kaawalii	0.37	88	0	3232.99		
2013							
	Honolii	8.24	30	15	1292.07	0.0	32.8
	Pahoehoe	0.60	0	34	1315.66	1.8	32.5
	Kolekole	3.46	9	19	2076.11	0.3	31.8
	Kapue	2.85	16	28	1907.81	13.3	0.0
	Umauma	2.09	18	8	4251.17	5.1	0.1
	Waikaumalo	1.67	46	6	4435.84	1.3	0.0
	Manoloa	0.59	27	10	958.90	0.4	22.5
	Makahiloa	0.28	44	13	1555.68	17.3	0.0
	Pahale	0.66	66	0	2684.30	5.6	0.0
	Manowaiopae	0.06	85	12	1600.13	20.5	0.5
	Kaawalii	0.28	100	0	2878.56	9.2	0.0
2014							
	Honolii	9.05	26	12	1434.31	0.7	30.0
	Pahoehoe	0.68	1	29	1901.82	4.6	34.8
	Kolekole	4.29	7	37	2269.36	3.8	24.0
	Kapue	3.37	9	33	2561.48	7.0	0.3
	Umauma	2.37	15	17	4534.51	15.6	0.0
	Waikaumalo	1.69	38	1	3988.10	2.3	0.0
	Manoloa	0.46	11	12	1257.19	21.1	10.9
	Makahiloa	0.30	70	6	2043.65	24.4	0.0
	Pahale	0.53	88	0	3071.37	30.9	0.0
	Manowaiopae	0.13	89	0	1990.08	13.0	0.0
	Kaawalii	0.26	84	0	3065.82	12.8	0.0

Table C2.4. Averages values of habitat factors from transect surveys

		Pahoe	Kole			Uma	Waikau	Maka		Mano-	Kaa-
	Honolii	-hoe	-kole	Kapue	Manoloa	-uma	-malo	-hiloa	Pahale	waiopae	walii
Average POCL (mm)											
2012	6.7	6.8	7.3	6.6	6.1	5.5	5.5	5.3			5.5
2013	6.5	7.3	7.3	6.8	5.9	5.7	5.5	5.5	6.0	5.2	5.4
2014	6.6	7.1	7.1	6.5	5.8	5.6	5.4	5.4	5.8	4.8	
Average relative mass (%)										
2012	94.5	110.2	105.5	97.7	107.0	93.4	95.1	93.7			84.1
2013	99.0	105.2	112.1	102.8	100.4	93.0	96.6	98.6	89.5	80.3	80.7
2014	101.5	120.1	108.8	109.7	109.9	104.1	112.2	111.8	106.6	95.2	
Brown spot disease (%)											
2013	1.6	0.0	2.9	0.0	17.1	8.9	2.4	5.2	12.9	2.6	20.5
2014	0.0	1.2	3.8	1.2	13.5	11.4	10.2	12.0	9.2	2.5	
Average biomass (g/m ²))										
2012	0.82	0.66	0.36	0.27	0.57	0.49	0.40	< 0.01	0.00	< 0.01	0.01
2013	0.80	0.78	0.43	0.20	0.12	0.33	0.23	0.00	< 0.01	< 0.01	0.09
2014	0.61	0.67	0.36	0.27	0.19	0.29	0.26	0.01	0.00	0.00	< 0.01

Table C2.5. Atyoida bisulcata population characteristics summarized for each reach each year.

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CHAPTER 3

SPATIAL PRIORITIZATION OF HAWAII'S STREAM ECOSYSTEMS FOR CONSERVATION IN THE CONTEXT OF CHANGING CLIMATE

Abstract

Declines in biodiversity resulting from anthropogenic disturbances to stream catchments and habitats have occurred at a global scale. Climate change threatens to exacerbate these effects, and in some cases, alter systems to the point where they can no longer support current assemblages of organisms. Spatial prioritization of streams that identifies habitats for protection or enhancement can aid in efforts to conserve stream habitats and their organisms with current and future threats. The goal of this study was to address this need for streams of the five largest Hawaiian Islands. Our first objective was to identify areas of high conservation priority by considering both current and future characteristics of stream habitats, with future characteristics determined by projected changes in rainfall at multiple time steps under multiple climate scenarios. To provide additional insight for prioritizing conservation action, we also assessed how future priority rankings compared to rankings based on current conditions. Our results indicate that many regions that currently have stream reaches of high conservation value will retain these characteristics through the end of the century under two different climate scenarios. In addition to ranking streams by their within-reach habitat value, we established the importance of connectivity to marine habitats in our ranking procedure, thus ensuring that complete migratory pathways for Hawaii's native amphidromous organisms were prioritized. Our results suggest that streams that drain leeward slopes of the islands will likely experience reductions in rainfall and may be negatively influenced by climate change. This study offers useful insight into potential effects of climate change on tropical island streams and helps inform the location and

type of conservation action that may be most effective to ensure the persistence of native Hawaiian stream organisms.

Introduction

Anthropogenic land use and alterations to stream channels including water diversions and dams have degraded stream habitats worldwide (Allan, 2004; Helfman, 2007). Disturbances to habitats have contributed to global declines in stream species biodiversity and increasing numbers of species at risk of extinction (Strayer et al., 2006; Helfman, 2007; Jelks et al., 2008). In addition, recent climate change has also had various impacts on stream organisms documented in multiple regions. Increases in air temperature and changes in precipitation have reduced population size and recruitment of salmonid fishes in North America (e.g., Ward et al., 2015; Bassar et al., 2016). Increases in water temperature have also increased disease prevalence and loss of habitat for Salmo trutta in alpine streams of Switzerland, contributing to declines in abundance (Hari et al., 2006). Climate-induced reductions in distributions of cold and cool water fish species have also been reported in multiple regions across the globe (as reviewed by Comte et al., 2013). Given that increases in air temperature and changes in precipitation are projected to continue over the coming century (IPCC, 2013), climate change effects on stream organisms will likely be magnified and exacerbate global reductions in biodiversity and increases in species at risk of extinction (Xenopoulos et al., 2005; Tedesco et al., 2013).

The current state of the world's streams combined with the likelihood of continued climate change underscore the need to consider both current and future disturbances when prioritizing stream habitats for conservation. Conservation prioritization efforts that only consider current conditions may not be fully effective at identifying priority habitats to protect at-risk species, as even pristine systems may change in their ability to support assemblages with

changing climate (e.g., Battin et al., 2007). It is therefore imperative to anticipate and utilize information on potential effects of climate change on stream habitats and organisms when prioritizing areas for conservation (Palmer et al., 2009; Zeigler et al., 2012). However, a recent review shows that a majority of spatial prioritization studies have not incorporated climate change as a potential source of disturbance, and of those that do, very few focus on streams (Jones et al., 2016). This underscores the need for additional regional efforts that support proactive conservation of stream habitats and organisms in the context of climate change.

Streams of the Hawaiian Islands are home to an assemblage of native shrimp, fish and snails, the majority of which are endemic to the island chain. Some of these organisms are also a traditional food source of Hawaiian people and are still harvested by island residents. Currently, anthropogenic land use and channel diversions have degraded many stream habitats, which has in turn reduced species abundances in select areas of the islands (Brasher, 2003; Walter et al., 2012). Due to their limited distributions and recent population declines, the International Union for Conservation of Nature (IUCN) lists several of these species as near threatened or vulnerable including *Atyoida bisulcata, Neritina granosa,* and *Sicyopterus stimpsoni* (World Conservation Monitoring Centre, 1996; Cordeiro & Perez, 2012; De Grave & Cai, 2013).

In recent years, conservation decision makers have prioritized Hawaiian streams for native species conservation based on estimates of current habitat condition and available species data (e.g., Hawaii Fish Habitat Partnership, 2010). However, a lack of downscaled projected climate data for the Hawaiian Islands has prevented past efforts from incorporating climate change into spatial prioritizations, therefore limiting the ability to implement proactive conservation strategies. This represents a critical knowledge gap for decision makers interested in prioritizing areas for conservation action, as declines in baseflow over the past century across

the island system have been attributed to reductions in mean annual rainfall (Bassiouni & Oki, 2013; Frazier & Giambelluca, 2016), suggesting that further declines in rainfall will have negative consequences for Hawaiian stream organisms. Recently, downscaled rainfall projections across the Hawaiian Islands have become available (Timm et al. 2015), and these projections indicate that climate change may result in substantial and regionally-specific reductions in total rainfall across Hawaii. Changes in the ability of streams to support a given taxa assemblage may occur as mean annual rainfall changes (Tingley this volume a), and where populations persist within streams, recent research suggests that moderate flow reductions and increased flow variability associated with lower rainfall can result in smaller individuals in poorer condition (Tingley this volume b).

The goal of this study is to incorporate projected climate data into a prioritization of stream habitats of the Hawaiian Islands for conservation of native species. Our first objective is to identify areas of conservation value by considering both current and future characteristics of stream habitats, with future characteristics determined by projected changes in rainfall. Completing this objective will allow us to identify streams that are likely to retain high conservation value given differences in climate change scenarios at different time periods. Our second objective is to assess how outcomes of future rankings of conservation value compare to a ranking based only on current condition to assess how prioritization strategies differ when accounting for projected climate change. The results of this study will highlight the importance of using proactive approaches when identifying high-value conservation areas while also providing information to decision-makers in Hawaii.

Methods

Study area

The study area included all perennial and intermittent stream reaches and their catchments from the five largest Hawaiian Islands (Hawaii, Maui, Molokai, Oahu and Kauai; Figure 3.1). Though regional variation in rainfall does occur throughout the islands, interactions between eastern trade-winds and topographic characteristics of each island control dominant rainfall patterns and result in generally higher precipitation at higher elevations on the windward (eastern) sides of islands and lower precipitation on leeward (western) facing slopes (Giambelluca et al., 2011). Groundwater contributions to stream flow are substantial in some catchments and near zero in others (Lau & Mink, 2006; Izuka et al., 2015). Disturbance from agricultural and urban land use in stream catchments tends to be more severe along coastlines and at lower elevations, while many high elevation areas are relatively undisturbed (Crawford et al., 2016).

Native Hawaiian stream organisms include five species of fish (four in the family gobiidae and one eleotridae), two shrimp (*A. bisulcata* and *Macrobrachium grandimanus*) and a neritid snail (*N. granosa*; Kinzie, 1990). All of these species are amphidromous; they hatch in streams, spend a short time (weeks to months) developing in the marine environment, and then migrate upstream to mature and reproduce (McDowall, 1988). Current research suggests that these species do not exhibit natal stream homing, and there is little distinguishable genetic structure across the study region (Chubb et al., 1998; McDowall, 2003; Bebler & Foltz, 2004). Coastal species, most notably striped mullet (*Mugil cephalus*) and flagtails (*Kuhlia sp.*), move to and from freshwater stream habitats (Nishimoto et al., 2007; McRae et al., 2011).

Study units

The spatial unit assessed through our rankings was the stream reach as defined in the Hawaii Fish Habitat Partnership (HFHP) stream layer (Tingley this volume a). The HFHP stream layer is a modified version of the 1:24,000 National Hydrography Dataset (NHD 2008; http://nhd.usgs.gov/) and includes 11,437 intermittent and perennial stream reaches delineated by hydrologic breaks within the river network (e.g., confluences with other stream reaches, waterfalls, and/or reservoirs). Each stream reach has an associated local catchment, defined as the portion of the landscape where surface runoff enters the reach directly, as well as an upstream catchment, defined as the entire area of the landscape draining to a given reach by other tributaries and including the local catchment (following Wang et al., 2011).

Ranking reaches based on current and future conservation value

We used the spatial prioritization software program Zonation version 4.0 (Moilanen et al., 2014) to generate multiple rankings of current and future conservation value of Hawaiian stream reaches. Zonation prioritizes spatial units based on their ecological uniqueness by accounting for presence of a habitat or species of interest (i.e., conservation features), disturbances to study units, and their connectivity to other study units. We generated five rankings with Zonation. We conducted one ranking of conservation value using only current conditions, and four additional rankings that characterized conservation value based on current conditions and projected changes in rainfall from two different downscaled climate change scenarios (RCP 4.5 and 8.5) at two time periods (mid- and late-century; Timm et al., 2015). Prior to ranking, we took multiple steps to define conservation value of individual reaches (Figure 3.2).

Defining reach conservation value based on uniqueness of ecological potential

Determining current ecological potential

Across the five main Hawaiian Islands, variation in natural landscape characteristics including average annual rainfall, reach elevation, channel slope, and catchment soil permeability results in a diversity of stream habitats within and across catchments (Tingley this volume a). The current ecological potential of stream reaches was defined based on results of a stream reach classification that associated the landscape factors listed above with distributions of stream taxa (Tingley this volume a). Thirteen classes of stream reaches were identified through the classification based on differences in types and specific values of landscape factors associated with differences in assemblages. For ranking, we considered classes that reaches occurred within to be ecologically unique habitats, and we used these classes as the conservation features of interest selected for within Zonation (Figure 3.3).

Determining future ecological potential

We estimated future ecological potential for the four future stream rankings using stream reaches reclassified based on summarized projected annual rainfall data. Downscaled projected rainfall data for Hawaii are currently available at two time periods (mid-century and late-century) for both medium-low (RCP 4.5) and high emission scenarios (RCP 8.5; Timm et al., 2015). We summarized projected annual rainfall data in the upstream catchment of stream reaches for each of the two emission scenarios at each time period using the aggregation tool described in Tsang et al. (2014). We then generated four representations of future classes by reclassifying reaches that had current rainfall associated with taxa distributions. Four of 13 classes met this criteria, and we considered these susceptible to climate change and likely to change in their ability to support current taxa assemblages (classes G, H, I, K; Table 3.1).

Creating and assigning the similarity matrix values to reaches

To ensure that rare habitats are not underrepresented in rankings of conservation value generated with Zonation, it is important to account for similarity among habitats (in our case, reach classes). We developed a measure of biological similarity for reach classes following Leathwick et al. (2010) based on prevalent native stream taxa comprising assemblages of each of the 13 stream reach classes (Table 3.1). Similarity values assigned to pairs of stream reach classes ranged from 0 (prevalent taxa for a stream reach class are fully distinct from taxa of another class) to 1 (all prevalent taxa are shared between two classes; Table C3.1). We then incorporated the resulting similarity matrix using the community analysis option in Zonation for our rankings (following Moilanen et al., 2014).

Creating and assigning taxa association weights to reaches

Because efforts to conserve streams in Hawaii have conservation of native stream organisms as a primary focus, we incorporated a biodiversity measure into our rankings. We developed a relative weighting of numbers of prevalent taxa within each reach class to account for differences in reach class biodiversity (Table 3.1). We assigned reach classes with five or more prevalent taxa a value of 4, classes with two to four taxa a value of 3, and classes with only one prevalent taxon a value of 2. Classes that did not support amphidromous species but that represent unique habitats still important for conservation (e.g., high elevation bogs) were assigned a value of 1. Intermittent streams were assigned a value of 0 because we assumed that these streams were least suitable for native Hawaiian stream organisms.

Modifying reach conservation value based on current and future disturbance

Applying current habitat condition score to estimates of conservation value

For the current conservation ranking using Zonation, we characterized disturbance to stream reaches using a landscape-scale assessment of stream habitats conducted across the five main Hawaiian Islands (Crawford et al., 2016). The assessment is based on the assumption that greater amounts of disturbance in stream catchments will result in greater disturbance to stream habitat (following Danz et al., 2007; Esselman et al., 2011). Assessment scores were derived from multiple measures of anthropogenic landscape and stream channel disturbances likely to have negative influences on habitat in stream reaches (Crawford et al., 2016), and results include disturbance scores as indices available in multiple spatial extents. To create our score, we summed an index characterizing fish habitat condition in local catchments of our stream reaches with a second index characterizing fish habitat condition in their upstream catchments. We then standardized this summed index to develop our cumulative upstream habitat condition index (UHCI) from 0 (worst habitat condition) to 1 (best habitat condition) for analysis. We incorporated the UHCI into the analysis for the current condition ranking using the "condition layer" option in Zonation, which modifies the value of each reach given its measure of habitat condition, up-weighting the conservation value of reaches with high UHCI scores in a given reach class. In the four future rankings, we used both the UHCI scores with the climate exposure score, described below, to modify reach conservation value.

Applying climate change exposure scores to estimates of future conservation value

Stream reach classes were defined based solely on the range of conditions characterized by current climate data, however, strong deviations from current climate could still yield novel conditions that could negatively affect stream organisms. To account for possible climate

changes beyond the range expressed by current conditions in our rankings, we generated a "climate exposure score" by identifying projected annual precipitation amounts in stream catchments that were substantially different from current conditions (Bush et al., 2014). We first summarized current (1992-2007) mean annual and dry season rainfall in the upstream catchment of stream reaches using monthly rainfall raster datasets developed by Frazier et al. (2015). We then found the average and standard deviation of current annual and dry season rainfalls for each stream reach. Next, using projected rainfall data, we determined whether mean annual and dry season rainfalls for a given time step and climate change scenario were greater than one standard deviation from current means. For those reaches where projected annual or dry season rainfalls were reduced by more than one standard deviation from current means, we assigned a value of 0.5, meaning their conservation value would be lowered given the potential exposure to climate change . Reaches that changed class with changes in climate were also assigned a value of 0.5, and all other reaches were assigned a value of 1.

Allowing reach conservation value to vary based on downstream connectivity

Creating and applying downstream habitat loss penalty

Given the amphidromous life histories of many Hawaiian stream taxa, the conservation value of a reach depends on its hydrologic connectivity to the marine environment. For each of the five Zonation reach rankings, we used information on stream network connectivity available in the HFHP stream layer to identify the portion of a stream network connecting the reach to the marine environment. We then used the neighborhood quality penalty (NQP; Moilanen & Kujala, 2008) to prioritize migratory pathways in each stream ranking. Following Bond et al. (2014), the value of a reach was set to be dependent on the conservation value of downstream reaches connecting the reach to the marine environment.
Ranking stream reaches based on conservation value

We used the Core-Area Selection (CAZ) procedure for all five conservation value rankings, given that this procedure is appropriate for studies in which priority units are those with the greatest amount of conservation features in the best condition (Leathwick et al., 2010). Priority ranking in Zonation begins with a representation of the entire landscape of interest and proceeds by the iterative removal of single study units that contribute the least conservation value until all study units have been removed (Di Minin et al., 2014). This results in the ranking of each individual study unit, in this case the stream reach, on a scale from 0 to 100%, with the reach ranking 100% having the highest conservation value, and the reach with 0% having the lowest conservation value.

When designing proactive conservation strategies based on projected conservation value, managers should consider results in the context of uncertainty associated with projected climate changes. Therefore, we examined overlap in the ranks of individual reaches across the study area for each of the projected climate scenarios at both mid and late century time periods. In some instances, we interpreted results by region (Figure 3.1) and examined regional differences with an emphasis on the top 5, 10 and 20% of overlapping ranked reaches. Reach ranking values were attributed to local catchments and mapped across the study region.

Assessing differences in prioritization when accounting for climate change

We compared stream reach rankings at each future time-period with current conservation value rankings to assess how proactive approaches to prioritization differ from approaches focused only on current condition by considering overlap in the top 5 and top 10% of reaches in each ranking. In addition, we identified those reaches that were only in the top 10% of the

current conservation value ranking or the future conservation value ranking for each time period. Results were attributed to local catchments and mapped across the study region.

Results

Changes in reach class and reductions in rainfall with climate changes

Changes in total length of stream reaches found within each reach class were projected to occur under both climate scenarios at each time period (Table 3.2). These changes suggest a shift in the ability of a stream reach to support its current assemblage of stream organisms. Overall, changes to classes were projected to be greater in the latter part of the 21^{st} century, and most changes were projected to occur in the Hilo/Hamakua and East Maui regions (Figures D3.1 – D3.4). Several high elevation reaches on the leeward sides of Kauai and Molokai were also projected to change classes. Across time periods and for each climate scenario, the total length of stream reaches classified as G, H and K were projected to decrease with changes in mean annual rainfall, while classes L and I were projected to increase. The greatest absolute change in total reach class length occurred to class I under the RCP 4.5 climate scenario (118 km gained), but the greatest change relative to current reach length occurred in class K under the RCP 8.5 climate scenario (73 of 233 km, or a reduction of ~31%).

Changes in average annual or dry season rainfall were projected to exceed one standard deviation from current estimates of mean annual rainfall for many stream reaches across the Hawaiian Islands (Table 3.2). Most changes in annual and dry season rainfall occurred under the late century RCP 8.5 scenario, with 2,419 km of streams projected to have mean annual rainfall values lower than one standard deviation from current values, and 3,174 km of streams projected to have mean rainfall declines. Projected negative changes in annual and dry season rainfall

were more common the leeward side of each island where many intermittent reaches occur (Figures D3.5 - D3.12).

Ranking reaches based on future conservation value

Mid-century time period

Overall, rankings of stream reaches based on mid-century projections suggest that each of the five islands will continue to support areas of high conservation value (Figure 3.4). The Kohala Mountains, northeastern Molokai, and the windward side of Kauai (denoted as Windward Kauai) had many reaches ranked in the top 5 and top 10%. In addition, these highlyranked reaches tend to extend up to high elevations and include complete stream networks. Less disturbed areas along the windward slopes of east and west Maui also contain several stream networks that have many reaches ranked in the top 5 and 10%. Windward Kauai had the largest percentage of total reach length within the top 20% of all ranked reaches across the islands (26.2%), followed by leeward Oahu (15.6%) and the Kohala Mountains (13.4%). Windward Kauai, Windward Oahu, and the Kohala Mountains had the highest percentages of total reaches ranked within the top 20% (33.8, 30.3 and 28.8%). This is likely a reflection of multiple factors, including a high percentage of perennial reaches within these regions, presence of less common reach classes, and relatively low UHCI and climate exposure scores. In addition, high ranking of low elevation reaches occurred in many areas across the islands, in some cases, even in stream networks where upstream reaches had low rankings (i.e., Windward Kauai). Considering the large number of perennial reaches along the north Hilo coast, a comparatively small percentage of reaches within the region were ranked in the top 20% (6.6%).

Late-century time period

Overall, the rankings of stream reaches using late-century climate scenarios were similar to those of the mid-century time period, but some regions were projected to have declines in conservation value (Figure 3.5). Leeward Kauai, for example, had no stream reaches ranked in the top 5%, and only 6 km of stream reaches ranked in the top 10% in the late-century ranking, compared to 7.8 and 29.3 km in the mid-century ranking (Table 3.3). Similar to the mid-century conservation value rankings, Windward Kauai, northeastern Molokai, and the Kohala Mountains had a high a proportion of stream reaches ranking in the top 5 and 10%, but windward Kauai had a greater length of reaches ranked in the top 10% compared to the mid-century rankings (239 vs. 277 km). However, several reaches along the southeastern Na Pali Coast show some declines in stream ranking. In addition, Molokai had 11.4 km fewer of stream reaches ranked in the top 5% in the late-century compared to the mid-century scenario (63.7 versus 52.3 km).

Differences in priority reaches in current vs. future rankings

Many of the reaches in the top 5 and 10% of the current conservation value ranking were also in the top 5 and 10% in both the mid and late-century rankings (Figures 3.6 and 3.7), but some notable differences occurred. For example, high elevation reaches of northeast Molokai were in the top 10% of reaches in the current conservation ranking, but were not in the top 10% in the mid and late-century rankings. In addition, reaches that drain leeward facing slopes on Kauai and West Maui were less commonly selected in the top 10% in future conservation value rankings than in the current conservation value ranking. Along the Hilo/Hamakua Coast of Hawaii, high elevation reaches were less commonly ranked in the top 10% in future rankings than in the current reach ranking. Along the windward coast of Oahu, however, several stream reaches were ranked in the top 10% only in future conservation value rankings while few were only selected in the top 10% in the current conservation value ranking.

Discussion

Given anticipated changes in climate, proactive strategies are needed to effectively conserve stream organisms (Palmer et al., 2009; Zeigler et al., 2012). In this study, we used best available information on the ecological potential of stream reaches, estimates of current habitat condition, and projected changes in rainfall to identify Hawaiian stream reaches of high conservation value under two future climate scenarios for two time periods. Summaries of projected average annual and dry season rainfall within upstream catchments of reaches indicate that many intermittent and perennial streams may be influenced by lower precipitation in the future. The results of our future ranking scenarios indicate that areas of high conservation value occur across all five of the largest Hawaiian Islands, and that several regions known to support important habitat for native stream organisms will likely continue to be of high value in the future, regardless of the climate scenario or time period considered. Comparison of future conservation value rankings with the current conservation value ranking indicates that leeward perennial streams and some high elevation reaches may lose value due to reductions in average dry season or annual rainfall and, in some cases, due to changes in the ability to support the assemblage of stream organisms that they currently support. Our results are particularly valuable for developing proactive stream conservation strategies in Hawaii because they can be used to consider the type and location of most effective conservation measures.

Ranking reaches based on current and future conservation value

The high ranking of many low elevation reaches across the study area results from migratory limitations of Hawaii's stream species as well as patterns in anthropogenic disturbance

to the catchment and channel. In this study, we defined conservation value as the ecological uniqueness of a stream reach and prioritized those reaches that supported more taxa. Because many low elevation reaches are associated with high numbers of unique taxa that are not likely to migrate far upstream, such as Stenogobius hawaiiensis and Macrobrachium grandimanus (Kido, 2008; Parham et al, 2009; Tingley this volume a), the relatively high ranking of low-elevation stream reaches is not surprising. In addition, land use and stream channel disturbance to Hawaiian streams tends to be most severe in low-elevation areas near the coast (Crawford et al., 2016). This limits the conservation value of many reaches in these areas, therefore magnifying the importance of those low-elevation reaches that are in moderate to good condition in the Zonation ranking procedure (De Minin et al., 2014). Application of the climate exposure score also lowered the conservation value of reaches where changes in ecological potential or declines in annual or dry season rainfall were projected to occur. This contributed to higher rankings of perennial reaches draining windward slopes, given the lower number of reaches in these regions projected to experience declines in rainfall as compared to leeward draining streams. This is perhaps most apparent in the high ranking of many low elevation reaches along Windward Oahu, which have lower UHCI scores than reaches in other regions but are unlikely to experience reductions in rainfall (Table 3.3).

Highly-ranked stream reaches at higher elevations were not common in the future rankings, but when they did occur, they were located in stream networks that were connected to the marine environment by other highly-ranked reaches. For instance, streams located on the north and northwest side of the windward coast of Kauai as well as in the Kohala Mountains region of Hawaii Island were highly ranked through the majority of their stream networks. In general, these regions contain low elevation reaches with low anthropogenic disturbance relative

to many other regions of the Hawaiian Islands (Crawford et al., 2016). The selection of reaches throughout these stream networks indicates that accounting for the condition of reaches in the downstream network in the ranking procedure effectively prioritizes streams that are likely to support complete amphidromous migratory pathways in good condition. In some regions, such as east Maui and on the island of Molokai, the prioritization of high elevation bogs may have also resulted in the selection of entire watersheds, given their relative uniqueness compared to other reach classes.

The future magnitude of greenhouse gas emissions is uncertain, but significant climate change is now considered inevitable, and the implementation of proactive conservation strategies requires that decisions be made despite uncertainty. Examination of overlap in reaches with high conservation value from both climate scenario rankings at a given time period allowed for identification of streams most likely to have high conservation value with changes in climate. Reaches that were highly ranked in both scenarios are those that are most likely to retain conservation value regardless of projected future climate change, suggesting that decision makers can prioritize protection of these reaches under the assumption that they represent the best opportunities to continue to support habitat for native stream organisms.

The comparison of rankings at the mid and late-century time periods offers two benefits. First, it demonstrates that changes in rainfall may have greater effects on the conservation value of specific reaches or regions as climate change progresses. For instance, a decline in conservation value in reaches that drain the leeward slopes of Kauai and West Maui is indicative of the "wet getting wetter, dry getting drier" outcome anticipated to be a general pattern in precipitation change at a global scale (IPCC, 2013). Second, because levels of human induced radiative forcing are relatively similar at the mid-century time period under all four of the RCP

scenarios (IPCC, 2013), use of the late-century projection demonstrates how differences in the magnitude of anthropogenic forcing may differentially affect the long-term conservation value of Hawaiian streams.

Differences in priority reaches in current vs. future rankings

Comparison of the current ranking with future rankings of conservation value demonstrates how accounting for changes in ecological potential and exposure to changing climate can affect conservation prioritization. Differences are most pronounced on the leeward sides of Kauai and West Maui, where many reaches are projected to experience declines in either annual or dry season rainfall, and sometimes both. Declines in the conservation value of these reaches likely contributed to observed increases in the ranking of reaches along windward sides of islands in areas that have ecologically similar reach classes to those that drain leeward slopes. Several reaches at high elevations on Molokai and in the Hilo/Hamakua region of Hawaii Island are ranked in the top 10% in the current condition ranking but not in future rankings. This is likely the result of a shift in the ecological potential of stream reaches resulting from projected changes in average annual rainfall, which will potentially alter the current ability of these streams to support current assemblages.

Implications for the proactive conservation of Hawaiian streams

Our results can be used to assess what conservation actions may be most effective in different regions of the Hawaiian Islands. Proactive conservation approaches that include preservation of habitats or establishment of protected areas may be most appropriate in regions where entire stream networks consist of highly ranked reaches under multiple climate scenarios. In addition, comparison of current and future rankings can aid in conservation decision making. For example, in streams projected to have reduced conservation value due to declines in average

dry season or annual rainfall, conservation approaches that support maintenance of current baseflow (i.e., prevention of additional water diversions) can increase the likelihood that these reaches retain habitat for native stream species in the future. In addition, if flow in these streams is currently diverted, as it is along much of west Maui (Cheng, 2014), the removal or reduction of water diversions may be an effective management action that buffers streams from future changes in climate. The identification of regions where many reaches were highly ranked only in future rankings can also help guide conservation actions. Streams in these regions may have lower habitat condition scores due to anthropogenic disturbance to the landscape and channel, but are unlikely to experience reductions in rainfall. This suggests that in regions like Windward Oahu, the restoration or rehabilitation of stream habitats may be an effective proactive conservation strategy.

Consideration of approach and future directions

Using multiple emission scenarios when conducting spatial prioritizations based on future conditions is necessary given the uncertainty associated with future climate change. While we addressed this in our approach by ranking reaches using two greenhouse gas emission scenarios, two additional scenarios (RCP 2.6 and 6.0) exist that are not currently downscaled for the Hawaiian Islands. We therefore recommend that when downscaled versions of these data become available, they be used in our spatial prioritization approach to offer decision makers a broader depiction of potential future conditions when developing proactive conservation strategies.

In this study, we used the finest resolution, statistically downscaled climate data available for the Hawaiian Islands. Statistical downscaling requires the assumption of "stationarity," meaning that current factors that control climate in a region remain the same through time

(Timm and Diaz, 2009). If regional controls on climate are altered as a result of climate change, biases in both the direction (i.e., increases vs. decreases in rainfall) and magnitude of projections developed using statistical downscaling will occur (Timm et al., 2015). Other approaches, such as dynamic downscaling, do not assume stationarity and will likely be available for the Hawaiian Islands soon (e.g., Zhang et al., 2016). Therefore, we suggest that as downscaled climate data are made available, additional rankings are developed using our approach and compared with the results of our study.

The climate exposure score was developed based on two factors: 1) whether a stream reach changed in class, therefore representing a shift in ecological potential and its ability to support native assemblages of organisms, and 2) whether it was projected to experience a reduction in average annual or dry season rainfall greater than one standard deviation from the current mean value. While the responses of stream flow and populations of stream organisms to differences in annual or dry season rainfall have not been studied explicitly in all regions of Hawaii, current research suggests that declines in rainfall will lead to declines in groundwater recharge and subsequent reductions in baseflow across the islands (Bassiouni and Oki, 2013). The assumption that any substantial reduction in rainfall will have negative consequences for stream organisms in Hawaii is well-founded, but increased study of specific effects of changes in the flow regime on stream organisms or stream habitat can be useful to increase our understanding of potential mechanisms by which climate change can impact streams.

The effective conservation of stream ecosystems requires that we continue to develop approaches that aid in prioritization of conservation actions in the face of changing climate. In this study, we incorporated the best available information on climate change effects on stream systems to identify areas for conservation and suggest specific conservation actions. Our results

draw attention to potential consequences of climate change for Hawaiian streams and provide a template for similar studies in other tropical island systems. In addition, this approach can be easily extended to include new information on ecological potential, current habitat condition and projected changes in climate. We therefore view our work as a building block for future studies that develop a dynamic picture of climate change effects in Hawaii, which can then be used to direct conservation actions to support the unique organisms of these stream ecosystems.

APPENDICES

APPENDIX 3.A

Tables

		Taxa	
Reach		association	
type	Description	weighting	Associated taxa
A	Coastal	4	S. stimpsoni, A. stamineus, N. granosa, E. sandwicensis, S. hawaiiensis, M. grandimanus, Kuhlia sp.
В	Low gradient downstream channel at low elevation	3	A. stamineus, M. grandimanus
С	High gradient downstream channel at low elevation	4	L. concolor, S. stimpsoni, A. stamineus, N. granosa, E. sandwicensis
D	Low gradient, moderate elevation, potential high water table	3	S. stimpsoni, A. stamineus
E	High gradient, moderate elevation, potential high water table	4	A. bisulcata, L. concolor, S. stimpsoni, A. stamineus, N. granosa
F	High gradient, high elevation, potential high water table	3	A. bisulcata, L. concolor
G	Moderate to high elevation, low rainfall	0	No taxa
Η	Moderate to high elevation, moderate rainfall	2	A. bisulcata
Ι	Moderate to high elevation, high rainfall	3	A. bisulcata, L. concolor
J	Terminal falls at low elevation	3	A. bisulcata, L. concolor
Κ	High elevation bogs	1	No taxa
L	Headwater reaches	1	No taxa
М	Intermittent reaches	0	No taxa

Table 3.1. Stream classes, taxa association weightings and taxa associated with each class resulting from the Hawaii stream reach classification. Associated taxa are defined by prevalence within a given class compared to prevalence across all samples reaches (Tingley this volume a).

Table 3.2. Changes in stream reach length for each class under each climate scenario and time period. Also shown are total lengths of stream reaches projected to be greater than one standard deviation from current mean annual or dry season rainfall under each scenario and time period.

	Class G	Class H	Class I	Class K	Class L	Annual rainfall (-/+ 1 standard	Dry season rainfall (-/+ 1 standard
Rainfall	(km)	(km)	(km)	(km)	(km)	deviation; km)	deviation; km)
Current	849	321	418	233	783		
Mid century							
RCP 4.5	-24	-71	96	-25	25	238/334	521/559
RCP 8.5	-24	-77	102	-36	36	477/316	1,334/547
Late century							
RCP 4.5	-40	-77	118	-41	41	573/570	909/589
RCP 8.5	-23	-87	110	-73	73	2,419/415	3,174/754

							Тор	Top 20%		Standard	
	Total	Perennial	Top	90.0-	80.0-	Тор	20% in	across	Mean	deviation	Range of
rea	ach length	length	>95.0%	94.9%	89.9%	20.0%	region	islands	UHCI	of UHCI	UHCI
Period Region	(km)	(km)	(km)	(km)	(km)	(km)	(%)	(%)	score	score	score
Mid-century rankings											
Island of Kauai	2215	1544	129	147	343	619	27.9	35.3	0.88	0.101	0.37-1.00
Leeward Kauai	856	582	8	29	122	159	18.6	9.1	0.87	0.072	0.44-1.00
Windward Kauai	1359	962	121	118	221	460	33.8	26.2	0.89	0.114	0.37-1.00
Island of Oahu	437	214	22	36	74	132	18.9	23.2	0.83	0.146	0.00-1.00
Leeward Oahu	1717	627	17	113	145	274	16.0	15.6	0.83	0.151	0.00-1.00
Windward Oahu	437	214	22	36	74	132	30.3	7.5	0.85	0.134	0.26-1.00
Molokai	964	230	66	57	48	168	17.4	9.6	0.97	0.053	0.62-1.00
Island of Maui	1870	574	34	74	109	218	11.7	12.4	0.91	0.101	0.53-1.00
West Maui	684	186	10	19	47	76	11.2	4.4	0.90	0.099	0.53-1.00
East Maui	1187	388	24	55	62	142	11.9	8.1	0.93	0.101	0.56-1.00
Island of Hawaii	3950	1819	72	88	184	342	8.7	19.5	0.86	0.117	0.35-1.00
Hilo/Hamakua	1884	1243	12	30	67	108	5.7	6.2	0.85	0.108	0.35-1.00
Kohala	814	569	60	58	117	234	28.8	13.4	0.85	0.126	0.47-1.00
Kona	1252	7	0	0	0	0	0.0	0.0	0.89	0.123	0.37-1.00
Late-century rankings											
Island of Kauai	2215	1544	133	150	331	614	27.7	33.8	0.88	0.101	0.37-1.00
Leeward Kauai	856	582	0	6	154	160	18.8	8.8	0.87	0.072	0.44-1.00
Windward Kauai	1359	962	133	144	177	454	33.4	25.0	0.89	0.114	0.37-1.00
Island of Oahu	437	214	24	35	66	125	18.6	22.1	0.83	0.146	0.00-1.00

Table 3.3. Total length of stream reaches that overlap in the top 20% of ranked reaches at each time period for the two climate scenarios. The percent of total reach length that is within the top 20% within a region and across islands as well as the mean, standard deviation and range of UHCI scores within a region are also shown.

Table 3.3. (cont'd)

re Period Region	Total each length (km)	Perennial length (km)	Top >95.0% (km)	90.0- 94.9% (km)	80.0- 89.9% (km)	Top 20.0% (km)	Top 20% in region (%)	Top 20% across islands (%)	Mean UHCI score	Standard deviation of UHCI score	Range of UHCI Score
Late-century rankings											
Leeward Oahu	1717	627	17	113	145	275	16.0	15.2	0.83	0.151	0.00-1.00
Windward Oah	u 437	214	24	35	66	125	28.5	6.9	0.85	0.134	0.26-1.00
Molokai	964	230	52	78	29	159	16.5	8.7	0.97	0.053	0.62-1.00
Island of Maui	1870	574	30	67	129	225	12.0	12.4	0.91	0.101	0.53-1.00
West Maui	684	186	10	25	54	89	13.0	4.9	0.90	0.099	0.53-1.00
East Maui	1187	388	20	42	75	136	11.5	7.5	0.93	0.101	0.56-1.00
Island of Hawai	i 3950	1819	64	126	228	418	10.6	23.0	0.86	0.117	0.35-1.00
Hilo/Hamakua	1884	1243	6	35	138	178	9.4	9.8	0.85	0.108	0.35-1.00
Kohala	814	569	58	91	90	240	29.5	13.2	0.85	0.126	0.47-1.00
Kona	1252	7	0	0	0	0	0.0	0.0	0.89	0.123	0.37-1.00

APPENDIX 3.B

Figures



Figure 3.1. The five Hawaiian Islands considered for spatial prioritization of stream reaches



Figure 3.2. Spatial prioritization approach taken for the ranking of stream reaches given current ecological potential and habitat condition and with projected changes in rainfall.



Figure 3.3. Reach classes used to estimate ecological potential (From Tingley this volume a). Intermittent streams not shown.



Figure 3.4. Spatial prioritization ranking of stream reaches under mid-century projected climate scenarios. Results were applied to local catchments for ease of interpretation. Rankings reflect those reaches that were above a given percentage in both scenarios.



Figure 3.5. Spatial prioritization ranking of stream reaches under late-century projected climate scenarios. Results were applied to local catchments for ease of interpretation. Rankings reflect those reaches that were above a given percentage in both scenarios.



Figure 3.6. Similarities and differences in the top 5 and 10% ranked sites under current condition and mid-century scenarios



Figure 3.7. Similarities and differences in the top 5 and 10% ranked sites under current condition and late-century scenarios

APPENDIX 3.C

Supplemental tables

Stream													
type	А	В	С	D	Ε	F	G	Η	Ι	J	Κ	L	Μ
А	1.00	0.29	0.50	0.29	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
В		1.00	0.29	0.33	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
С			1.00	0.40	0.67	0.17	0.00	0.00	0.11	0.11	0.00	0.00	0.00
D				1.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E					1.00	0.40	0.00	0.20	0.40	0.40	0.00	0.00	0.00
F						1.00	0.00	0.50	1.00	1.00	0.00	0.00	0.00
G							1.00	0.00	0.00	0.00	0.00	0.00	0.00
Н								1.00	0.50	0.50	0.00	0.00	0.00
Ι									1.00	1.00	0.00	0.00	0.00
J										1.00	0.00	0.00	0.00
Κ											1.00	0.00	0.00
L												1.00	0.00
М													1.00

Table C3.1. Similarity matrix applied to stream reach classes

APPENDIX 3.D

Supplemental figures



Figure D3.1. Changes in stream class under RCP 4.5 climate scenario for the mid-century time period.. "Negative" refers to a change in class resulting from a decline in rainfall, while "Positive" indicates a change in class resulting from an increase in rainfall.



Figure D3.2. Changes in stream class under RCP 4.5 climate scenario for the late-century time period.. "Negative" refers to a change in class resulting from a decline in rainfall, while "Positive" indicates a change in class resulting from an increase in rainfall.



Figure D3.3. Changes in stream class under RCP 8.5 climate scenario for the mid-century time period.. "Negative" refers to a change in class resulting from a decline in rainfall, while "Positive" indicates a change in class resulting from an increase in rainfall.



Figure D3.4. Changes in stream class under RCP 8.5 climate scenario for the late-century time period.. "Negative" refers to a change in class resulting from a decline in rainfall, while "Positive" indicates a change in class resulting from an increase in rainfall.



Figure D3.5. Stream reaches that increased or decreased by greater than one standard deviation from current conditions. during the dry season under the RCP 4.5 climate scenario for the mid-century time period.



Figure D3.6. Stream reaches that increased or decreased by greater than one standard deviation from current conditions. during the dry season under the RCP 4.5 climate scenario for the late-century time period.



Figure D3.7. Stream reaches that increased or decreased by greater than one standard deviation from current conditions. during the dry season under the RCP 8.5 climate scenario for the mid-century time period.



Figure D3.8. Stream reaches that increased or decreased by greater than one standard deviation from current conditions. during the dry season under the RCP 8.5 climate scenario for the late-century time period.


Figure D3.9. Stream reaches that increased or decreased by greater than one standard deviation from current annual mean annual rainfall under the RCP 4.5 climate scenario for the late-century time period.



Figure D3.10. Stream reaches that increased or decreased by greater than one standard deviation from current annual mean annual rainfall under the RCP 8.5 climate scenario for the mid-century time period.



Figure D3.11. Stream reaches that increased or decreased by greater than one standard deviation from current annual mean annual rainfall under the RCP 8.5 climate scenario for the late-century time period.



Figure D3.12. Stream reaches that increased or decreased by greater than one standard deviation from current annual mean annual rainfall under the RCP 4.5 climate scenario for the mid-century time period.

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CHAPTER FOUR

CONCLUSIONS: SUMMARY OF FINDINGS AND IMPLICATIONS FOR MANAGEMENT

In this chapter, I synthesize findings described in Chapters 1, 2 and 3. In addition, I describe potential management implications for each chapter, with an emphasis on the conservation of Hawaiian streams and their native organisms.

Principal findings

Chapter One: Influences of natural landscape factors on tropical stream organisms: An ecological classification of Hawaiian Island streams

Using currently available and newly developed spatial datasets, I explored influences of natural landscape factors on distributions of native stream taxa, which provided insight into the ecological potential of stream reaches across the Hawaiian Islands for supporting those taxa. My results indicate that stream size, channel slope, elevation, soil permeability, annual rainfall, and waterfall height all explained a substantial amount of variance in distributions of stream taxa in Hawaii. I then used a conditional inference tree to group stream reaches based on influences of individual natural landscape factors on taxa distributions, which resulted in groupings defined by differences in elevation, rainfall, channel slope and soil permeability. I used these results to develop a classification of 13 stream classes that, when extrapolated across the study region, spatially identify differences in the ecological potential of stream reaches. My study culminated in the first stream reach-scale ecological classification for the Hawaiian Islands. My approach effectively integrated existing knowledge on influences of natural landscape characteristics on distributions of stream organisms with new insight into important factors influencing taxa distributions at the reach scale. This study demonstrates the utility of implementing a landscape approach when assessing effects of natural landscape factors on stream organisms.

The results of this study also suggest that sensitivity of stream reach ecological potential to changing climate in Hawaii will depend on both relative exposure to change (i.e., the magnitude of change in rainfall) and the underlying characteristics of the natural landscape. Three stream classes associated with differences in organism distributions were all grouped based on statistically significant relationships with mean annual rainfall. These climate-sensitive classes occur at moderate to high elevations and likely lack substantial contributions of groundwater to baseflow, as suggested by comparatively lower soil permeability in their catchments. This suggests that stream reaches within these classes may change in their ecological potential if mean annual rainfall changes with climate change. Overall, my results add new insight into the sensitivity of stream habitat in Hawaii to changes in climate.

Chapter Two: Anticipating the effects of changing climate on tropical island streams: Influences of stream flow on atyid mountain shrimp

I assessed differences in population characteristics of an endemic mountain shrimp, *Atyoida bisulcata*, across 11 study streams with similar geology, topography, land cover, elevation and soil characteristics but that differed substantially in mean annual rainfall. I summarized daily stream flow data from each of the streams to assess differences in the flow regime across sites and years. My results indicate that mean annual rainfall has strong associations with multiple aspects of the flow regime including baseflow, flow variability, and frequency and duration of flow events. Several of these flow metrics were also strongly associated with habitat types available to *A. bisulcata*. Based on relationships between baseflow and measures of average size and relative mass, I determined that individual *A. bisulcata* in streams with lower baseflow are generally smaller and in poorer condition than in streams with higher baseflow. Baseflow and the frequency of low flows were also associated with differences

in biomass, which was highest in streams with the highest baseflow and approached zero in several reaches where low flows were frequent. Observed differences may be related to temporary habitat desiccation, less food availability or higher water temperature stream resulting from lower baseflow. I also documented increasing prevalence of the carapace infection brown spot disease in streams with greater flow variability. My results suggest that even moderate reductions in rainfall may affect populations of native stream organisms through changes to multiple aspects of the flow regime. This highlights the importance of considering measures beyond the presence or absence of species when assessing potential effects of changing climate on stream organisms.

Chapter Three: Spatial prioritization of Hawaii's stream ecosystems for conservation in the context of changing climate

Using information on the ecological potential of stream reaches, current habitat condition and projected changes in rainfall, I implemented a spatial prioritization approach that culminated in the ranking of stream reaches based on estimates of current and future conservation value for two time periods. Overall, my results indicate that areas of high conservation value will occur on all five of the largest Hawaiian Islands under both moderate and high emission scenarios. Despite projected changes in rainfall, many regions that are currently considered to be of high conservation value will likely continue to be of high value through the 21st century when considering climate change as the only driver. A comparison of rankings at mid to late-century time periods indicates that streams that drain leeward slopes may have limited conservation value due to substantial reductions in rainfall, and the severity of this effect will be dependent on future greenhouse gas concentrations. A comparison of rankings generated with future conditions to rankings generated only with current conditions indicated that leeward perennial streams may lose value in the future due to reductions in average dry-season and annual rainfall. My results highlight the importance of considering future effects of climate change when developing strategies for stream conservation. Further, these collective findings can provide guidance for conservation strategies across the Hawaiian Islands.

Management implications

Chapter One

My results show influences of natural landscape factors on taxa distributions and allow for a representation of ecological potential of reaches across the Hawaiian Islands. The development of an ecological classification from these results allowed for a visual representation of locations of rare and common habitats across all streams in Hawaii. When paired with data describing habitat condition of stream reaches resulting from anthropogenic disturbances, the classification can be used to assess the relative condition of different habitats, which has utility when considering the value of particular conservation actions. In addition, by broadly controlling for natural variation across the study region, the reach classification can be valuable in selecting sites for examining effects of landscape or channel disturbance on existing populations of stream organisms.

The classification also highlights the sensitivity of particular regions of Hawaii to changes in climate. For instance, streams of northeast Maui and the Hilo/Hamakua coast of Hawaii Island include many reaches that are classified based on differences in mean annual rainfall, suggesting that streams in these areas may be sensitive to reductions in rainfall. Therefore, conservation actions should be taken to maintain and restore as much flow as possible to these reaches to retain their ecological potential and buffer them against future climate change.

The classification is an effective way to represent differences in habitat across Hawaii, but we also recognize that certain stream habitats (i.e., high elevation reaches, hard to access reaches deep within stream valleys) may be underrepresented in the biological dataset. Therefore, targeted sampling efforts in these regions may help identify additional landscape influences on stream taxa not captured in the presence/absence database used in this study which can further improve the value of the classification to management. In addition, my study identified relationships between multiple natural landscape factors that have significant correlations with the distribution and abundance of stream organisms, which in some cases draws attention to important data needs across Hawaii. For instance, upstream minimum hydrologic soil grouping effectively captured upstream contributions of groundwater to baseflow from high elevation dikes, but geologic anomalies in Hawaii may result in site-specific differences in groundwater resources (e.g., perched groundwater; Izuka et al., 2015). The development of an island-wide spatial data layer describing groundwater delivery or identifying unique geologic features comprehensively across the islands could be beneficial to improving understanding of site-specific ecological potential.

Chapter Two

Observed declines in the condition and size of individual *A. bisulcata* with diminishing flow are indicative of the vulnerability of Hawaiian stream organisms to reduced baseflow. Protecting streams in Hawaii from water diversions or other disturbances that may reduce baseflow is a major focal point for management in Hawaii (Nishimoto & Fitzsimons, 2006). My results suggest that populations of stream organisms will be in the best condition when baseflow is highest, implying that efforts should be taken to maintain and restore flows to streams and not simply manage for minimum flows. Given that populations of *A. bisulcata* were largest and

biomass was greatest in streams with highest flows, I infer that reductions in baseflow may have negative effects on populations of *A. bisulcata*. This information can help direct management action (e.g., preservation vs. restoration) when paired with projected rainfall data.

In this study, I focus on a single species endemic to the Hawaiian Islands, but my results indicate that effective conservation requires continued research on effects of changes in the stream flow regime on populations of other Hawaiian stream organisms. While I broadly generalize that reductions in stream flow may influence other species, understanding specific effects of the flow regime on other species will improve conservation efforts. Using the classification of stream reaches developed in Chapter 1 to account for patterns in natural variability can be valuable in determining areas where observational studies like the one described in this chapter can be used to assess finer resolution changes to populations of other Hawaiian stream organisms. In addition, many tropical island systems support similar species assemblages to that of Hawaii, suggesting that my results may be broadly applicable for understanding effects of declining baseflow and increasing flow variability on other species found in tropical island streams.

Chapter Three

The results of this study demonstrate the importance of considering changes in climate when assessing the conservation value of streams in Hawaii. Streams in Hawaii and the organisms they support are sensitive to reductions in rainfall. Therefore, considering future changes in rainfall is an essential component when developing proactive conservation strategies. The high ranking of many stream reaches that drain windward slopes under multiple climate scenarios at different time periods indicates that these areas are likely to retain high conservation value regardless of projected changes in rainfall. This result suggests that establishing protected

areas or preserving catchments with many high ranking reaches may be an effective form of conservation. Areas that are ranked lower in future rankings when compared to the ranking based on current conservation value may be more suitable for conservation actions that restore or retain current flow, thereby buffering streams from anticipated effects of reduced rainfall. Finally, those reaches that increase in conservation value and are currently moderately degraded may be ideal locations for restoration actions that improve habitat, as they will likely be minimally affected by future changes in rainfall.

While I focus on protection of total native stream biodiversity in my prioritization analysis, the flexibility of my approach does allow for more targeted rankings that consider specific reach classes or species of interest for conservation. For instance, researchers interested in protection of *Lentipes concolor*, an endemic stream goby found in high elevation reaches, could alter my prevalent taxa association weights and adjust climate exposure scores to favor habitats that may support this species in the future. Furthermore, additional climate data from dynamic downscaling approaches will become available in the near future (as described in Zhang et al., 2016), thus offering further information to decision makers considering conservation measures in Hawaii.

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