CHARACTERIZING THE STREAM ENVIRONMENTS ASSOCIATED WITH INTRODUCED SPECIES ACROSS SPATIAL SCALES IN HAWAIʻI

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Abstract

Introduced freshwater species are among the most significant threats to native biodiversity worldwide. In Hawaiʻi, introduced stream species impact native populations through predation, competition, habitat alterations, and exposure to parasites and diseases. This study utilized biological and in-stream environmental survey data collected by state researchers and landscape variables from the 2015 National Fish Habitat Partnership assessment to assess habitat use and distribution of introduced stream species throughout Hawaiʻi. Surveyed in-stream environmental attributes (e.g., temperature, substrate, dissolved oxygen) were examined to determine the use of in-stream attributes of introduced species. Associations between landscape metrics and species were investigated using both natural and anthropogenic variables, assessed at multiple spatial catchments. Prominent associations with in-stream attributes included water temperature, depth, and substrate type. Species-landscape metric associations indicated that natural variables including downstream slope, elevation, and upstream rainfall, as well as anthropogenic variables including local and upstream population were important landscape predictors of species presence. Stream reach suitability of species was modeled for selected introduced stream species based on their observed occurrences throughout Hawaiʻi using important landscape scale factors. Areas with the greatest suitability among taxa included the low-sloped and low-elevation areas of Oʻahu, windward Kauaʻi, and central Maui, as well as select streams on Molokaʻi and Hawaiʻi Island. Information on species environmental associations at different spatial scales will improve understanding of biological invasions in tropical island ecosystems. This served to inform future management strategies on prioritization of streams for conservation and introduced species removal.

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List of Acronyms

ACOE – Army Corps of Engineers
AIC – the Akaike Information Criterion
AUC – Area Under the Curve
BRT – Boosted Regression Tree
CCA – Canonical Correspondence Analysis
CCAP – Costal Change Analysis Program
CERCLIS – Comprehensive Environmental Response, Compensation, and Liability Information System
DAR – Division of Aquatic Resources
DLNR – Department of Land and Natural Resources
DO – Dissolved Oxygen
EPA – Environmental Protection Agency
HFHP – Hawaiʻi Fish Habitat Partnership
GIS – Geographic Information System
ICIS – Integrated Compliance Information System
MRP – Mineral Resource Program
NED – National Elevation Dataset
NFHP – National Fish Habitat Partnership
NHD – National Hydrography Dataset
NOAA – National Oceanic and Atmospheric Administration
NRCS – National Resource Conservation Service
PCA – Principal Component Analysis
PCS – Permit Compliance System
SSURGO – Soil Survey Geographic Database
TIGER – Topologically Integrated Geographic Encoding and Referencing
TITAN – Threshold Indicator Taxa Analysis
TMDL – Total Maximum Daily Load
USGS – United States Geological Survey

Chapter One - Introduction

1.1 Background

1.1.1 Introduction

Introduced species are among the most significant threats to freshwater ecosystems worldwide (Leprieur et al. 2008), as they can alter community structure, ecosystem function, and native biodiversity (Holitzki et al. 2013). In the state of Hawai‘i, there have been more than fifty introduced species detected in freshwater environments (Yamamoto & Tagawa 2000), with at least one introduced species found in all perennial streams surveyed in a past state-wide assessment (Hawaii Stream Assessment 1991). Species introductions to freshwater environments in the Hawaiian Islands historically occurred in four waves (as summarized in Maciolek 1984, Devick 1991, Eldredge 1992, Brown et al. 1999). Prior to 1900, a number of species were introduced by Asian immigrant workers, primarily for food. Between 1900 and 1945, introductions largely occurred for mosquito control and recreational purposes. From 1946 to 1961, various species were introduced for the control of aquatic plants, for aquaculture, as bait fish, and for recreational purposes. From 1962 to recent, introductions primary occurred from amateur home aquarium owners releasing pets into streams and other freshwater environments.

The impacts of introduced species in Hawai‘i's freshwater ecosystems are largely unknown due to a lack of scientific-tested studies (Brown et al. 1999). However, information based on surveys, local knowledge, and the effects of these introduced species in other geographic locations suggest that many introduced species are a primary threat to native species and ecosystems (Brasher et al. 2006). Hawaiian streams are unique freshwater ecosystems, with limited diversity of native species and extreme environmental gradients, the impacts of introduced species could be severe. Additionally, many regional studies within the state suggested the expansion of introduced species ranges since their introductions (Timbol & Mackiolek 1978, Hawaii Stream Assessment 1991, Brasher et al. 2006). Currently, the control and management of introduced stream species in Hawai‘i is non-existent due to lack of information. There is a critical need to evaluate species distributions and the associated environmental factors across spatial scales. This information will allow for the development of management and control strategies and prioritization of stream conservation areas.

1.1.2 Stream ecosystems in Hawai‘i

In Hawai‘i, streams are short and drainage basins are small compared to continental freshwater systems. Streamflow characteristics are the result of different drainage basin factors including rainfall patterns, topography, drainage size, soils, and land use. Typical Hawaiian streams are often described as "flashy", meaning that water level can rise and fall several feet over a few hours in response to rainfall (Oki & Brasher 2003). This flashy nature is due to high-intensity rainfall, small drainage basins, steep basins and channel slopes, and little channel storage (Oki & Brasher 2003). Native species are well adapted to these large fluctuations in streamflow (McDowall 1995), whereas these conditions are thought to be intolerable for many introduced species (Fitzsimons et al. 1997, Brown et al. 1999, Englund et al. 2000a). Within a stream, this "flushing-out" capacity is typically expected to increase with elevation, as the controlling factors change, e.g., increasing rainfall and slope. Therefore, it is hypothesized that gradients of natural landscape factors such as elevation, rainfall, and channel slope limit the in-stream environmental suitability for introduced species.

The native stream fauna consists of five fishes, two crustaceans, and three mollusks, and numerous aquatic insects (Englund et al. 2000a, McDowall 2003). The native species (excluding insects) are phylogenetically derived from marine ancestors (McDowall 2007) and have retained a marine larval stage as part of their amphidromous life history. Amphidromy is characterized by adult life and reproduction occurring in streams, where newly hatched larvae drift downstream to the ocean where they spend several months as marine plankton (McDowall 2007). Post-larvae, i.e., juveniles, return to streams where they continue to grow before reproducing. This life history allows successive generations to disperse to watersheds not accessible by adults, permitting gene flow between populations and recolonization after disturbance events. The disadvantage of this life history is that it requires corridors connecting larval and adult habitats to be maintained. Furthermore, migrations leave native species susceptible to threats located outside of their immediate adult habitat, such as downstream introduced species (e.g., predation) and stream alterations (McDowall 2007). Additionally, native stream species are especially vulnerable to introduced species when they co-occur, due to the isolated evolution of native species that resulted in limited exposure to biotic forces of predation and competition (Loope et al. 2001, Staples & Cowie 2001). Native stream communities appear to be structured longitudinally by species-specific abilities to migrate upstream (Walter et al. 2012), this is thought to be largely determined by differing abilities to climb waterfalls (Keith 2003). Similarly, the occurrence and height of waterfalls have been hypothesized to limit the upstream dispersal of introduced species (Glenn Higashi, Hawaiʻi Department of Land and Natural Resources, personal communication).

1.1.3 Stream alterations in Hawaiʻi

Many Hawaiian streams have been altered by human activities creating degraded stream conditions that are more advantageous to environmentally-tolerant introduced generalist species compared to the relatively specialized native species (Norton et al. 1978). In the state of Hawaiʻi, stream alterations that influence stream environments and the associated biota occur at different spatial scales. Direct and localized alterations include stream channelization and diversions (Brasher 2003). While, indirect and large-scale alterations include urbanization and agriculture land use (Brasher 2003).

The most prominent localized alterations are stream channelization, which entails the artificial straightening of stream channels, and commonly includes concrete lined channels and the removal of riparian vegetation. Stream channelization projects are commonly associated with urbanized areas where they are implemented for flood control, but also occur in sparsely-developed areas for road crossings over streams (Brasher 2003). In Hawaiʻi, urban development and road crossings and the associated channelization, are primarily concentrated in low elevation, coastal areas (Brasher et al. 2006). As of 1978, greater than 19% of perennial streams throughout the state had been channelized to some degree (Hawaii Stream Assessment 1991), with the majority of concrete lined channels occurring on Oʻahu (Timbol & Maciolek 1978). Channelized streams are generally associated with decreased substrate heterogeneity, variability in channel units (e.g., riffle-run-pool complexity), water depth, and canopy cover (Brasher 2003). Collectively, these conditions lead to increased stream temperatures, light exposure, algal growth, and the consequential diel fluctuations in dissolved oxygen (Brown et al. 1999), which ultimately result in degraded stream environments that are more conducive to introduced species.

At larger scales, urbanization and agriculture contribute to altered stream conditions including flow regimes and decreased water quality (Brasher 2003, Allan 2004). Urbanization commonly results in increased pollutants, more erratic hydrology due to increased impervious surfaces, increased water temperatures due to decreased riparian vegetation, and a reduction in environmental heterogeneity (Allan 2004). Agricultural land use typically influences stream environments via a reduction of substrate heterogeneity due to increased erosion due to poor bank stability, as well as increased nonpoint pollution inputs such as fine sediments, nutrients, and pesticides (Allan 2004). Agricultural areas may also contribute to altered flow regimes and increased stream temperatures (due to decreased riparian area) depending on the agricultural area size, management practices, and proximity to streams (Allan 2004).

There are few studies that investigated the interaction between degraded physicochemical and geomorphological stream conditions and the prevalence of introduced species in Hawaiʻi. Brasher et al. (2006) evaluated the biological communities and in-stream environmental quality between developed and undeveloped stream sites across three islands (Kauaʻi, Oʻahu, and Hawaiʻi). Streams in undeveloped sites had higher streamflow velocities, more riffle channel units, lower substrate embeddedness, deeper water, and lower temperatures compared to developed sites. The developed sites were dominated by introduced species, and primarily located at low elevations. In an inventory of 48 streams across the five main Hawaiian Islands, and Mackiolek (1978) found that native species were dominant (in abundance and biomass) in most unaltered streams, while introduced species were dominant in channelized streams. However even though the relationship between the degree of stream alteration and the distribution of introduced species has been established in Hawaiʻi, little has been studied on their use of in-stream environments and their association the landscape gradients in Hawaiʻi. There is a need for analysis that considers how stream alternations at different spatial scales interact with natural factors (e.g., slope, elevation, waterfall) to influence the distribution and dispersion of introduced species. Additionally, environmental tolerances vary among species and species distributions may change through time. Species-specific evaluations which include recent survey records would greatly improve the ecological knowledge of introduced species in Hawaiʻi. Knowing the types of stream environments that support the kinds of introduced species would better assist the management design for introduced species control.

1.1.4 Introduced stream species in Hawaiʻi

A few prominent introduced species have been identified in previous studies based on their occurrence and perceived impact to native stream species and ecosystems. Poeciliid fishes (e.g. *Poecilia* spp., *Gambusia* spp., and *Xiphophorus* spp.) were widely introduced for mosquito control or via home aquarium owners (Yamamoto & Tagawa 2000) and are now among the most common introduced species found in Hawaiian streams (Walter et al. 2012). Poeciliids are likely predators of native stream species larvae (Walter et al. 2012) and native damselflies (Englund 1999). Additionally, these fishes have been found to compete with native fishes for food resources (Holitzki et al. 2013) and to transmit non-native parasites to native fishes (Font & Tate 1994). Poeciliids are viviparous that are capable of rapid population growth and dense populations. They commonly dominate altered streams as they are generally tolerant of thermal stress, hypoxia (Water et al. 2012), and salinity (Martin et al. 2009).

The Tahitian Prawn (*Macrobrachium lar*) was introduced to Molokaʻi in 1956 as food resource (Yamamoto & Tagawa 2000), and has since spread widely throughout the state (Hawaii Stream Assessment 1991). The amphidromous life history of this species allowed it to colonize new streams via planktonic larvae similar to native species (Englund et al. 2000a). The Tahitian Prawn directly feeds on native fish and native mollusks (Brown et al. 1999, Englund et al. 2000a). Additionally, the Tahitian Prawn competes for space and food resources with native species (Layhee et al. 2014), specifically the native crustacean ʻOpae ʻOehaʻa (*Macrobrachium grandimanus*) (Eldredge 1994). In addition to its wide distribution in the Hawaiian Islands, the species has been documented to possess some climbing ability which may allow the species to overlap with native species in a larger range compared to other introduced species (Yamamoto & Tagawa 2000).

Introduced suckermouth catfishes (family *Loricariidae*) likely introduced from home aquarium releases (Yamamoto & Tagawa 2000), burrow in stream banks causing increased erosion and turbidity (Brasher 2003). Suckermouth catfishes are large, herbivorous, benthic fishes that occur in extremely high densities in streams where they occur (Englund et al 2000a). These catfishes exhibit facultative air breathing which may allow populations to become established in streams with low water quality (Brown et al. 1999). Given the size and densities of these fishes, they could potentially become a major competitor to native fishes if their distribution expands (Brasher et al. 2006).

Various tilapia species (*Oreochromis* spp., *Tilapia* spp., *Sarotherodon* spp.) were introduced throughout the second half of the 19th Century for baitfish, aquatic plant control, food, and recreational purposes (Englund et al. 2000a, Yamamoto & Tagawa 2000). Today approximately ten different tilapia species are known to be established throughout the state (Yamamoto & Tagawa 2000). Generally, tilapia are tolerant of a wide range of environmental conditions, such as high temperatures, turbidity, salinity, and are additionally tolerant of polluted waters, including hypoxic, acidic, and alkaline conditions (Rappaport et al. 1976, Murthy 1981, Bhaskar & Govindappa 1986, Senguttuvan & Sivakumar 2002). Tilapia are generally considered aggressive fishes that are primarily herbivores, detritivores, or planktivores, but have been documented to consume fish larvae, small invertebrates, and small fishes (Bowen 1982, Arthington et al. 1994). Additionally, it has been suggested that large populations can increase bank erosion and water turbidity via grazing and courtship behaviors (Cooper & Harrison 1992), leading to a decrease in stream environmental quality and potentially primary production food resources for native species. The Blackchin Tilapia (*Sarotherodon melanotheron*) is of particular concern due to its diverse dietary preferences, requirements for large amounts of food, and high salinity tolerance. By 1999, this species was found in high densities in Oʻahu estuaries (Englund et al. 2000a) and lower stream reaches Oʻahu and some locations on Kauaʻi (Brown et al. 1999). The high salinity tolerance of this species may allow it to cross saltwater barriers and colonize neighboring streams (Brown et al. 1999). This fish is thought to heavily impact native species through competition and predation (Brown et al. 1999). Additionally, this species is perceived as a major cause of native waterbird decline due to intense competition for aquatic vegetation and invertebrates (Englund et al. 2000a).

Predatory and aggressive fishes such as centrarchid black basses (*Micropterus* spp.) and cichlids other than tilapias pose another threat to native species by direct predation and competition for food resources (Brasher 2003). Smallmouth Bass (*Micropterus dolomieui*) and Largemouth Bass (*Micropterus salmoides*) were introduced to the islands of Oʻahu and Kauaʻi in the 1950s for sport fishing (Yamamoto & Tagawa 2000). Smallmouth Bass are of particular concern because they are well adapted for the flashy streamflow conditions of Hawaiian streams and have significantly expanded their ranges within the watersheds which they were introduced (Brown et al. 1999). Additionally, the species popularity as a sport fish may lead to future introductions. There have been at least nine cichlids introduced into Hawaiian waters, most of which occurred in the 1980s and 1990s due to aquarium releases (Yamamoto & Tagawa 2000). The Banded Jewel Cichlid (*Hemichromis elongatus*) and Convict Cichlid (*Archocentrus* *nigrofasciatus*) have been suggested as the primary threats to native stream species based on their aggressive behavior and more frequent occurrence relative to other cichlids (Hawaii Stream Assessment 1991, Yamamoto & Tagawa 2000).

The Red Swamp Crayfish (*Procambarus clarkii*) was first introduced to taro fields on Oʻahu in 1923 (Brock 1960) by the government as a food resource (Englund et al. 2000a). After the introduction, crayfish populations grew rapidly, and became a serious pest to taro cultivation (Devaney et al. 1982). Chemical controls were used to reduce crayfish population within taro fields from 1940 to 1952 (Devaney et al. 1982). The Red Swamp Crayfish has become established throughout Hawaiʻi and is especially abundant on the south shores of Oʻahu (Englund et al. 2000a). In California, it has been reported to cause the displacement of native species (Shafland 1991). In Hawaiʻi, crayfish have been documented to prey on insects and mollusks (Devaney et al. 1982), however the effect on native fish and other native species is unknown.

A number of frogs and turtles have been introduced to freshwater environments in Hawaiʻi. Of these, the American Bullfrog (*Rana catesbeiana*) is thought to pose the most significant threat to native species (D. Polhemus, U.S. Fish and Wildlife Service, personal communication). The American Bullfrog was introduced to the island of Hawaiʻi in 1879 for the control of Japanese beetles and later utilized as a food resource (Englund et al. 2000a). The bullfrog has since spread throughout the main Hawaiian Islands (Yamamoto & Tagawa 2000). This frog is a highly predaceous opportunist feeder (Snow & Witmer 2010). Additionally, the American Bullfrog is able to temporarily move over land (Gahl et al. 2009), which may permit dispersal to previously non-invaded watersheds. The species has been reported to disperse long distances (e.g., maximum distances of approximately one km; Smith & Green 2005); however, there is insufficient evidence to determine how far bullfrogs can disperse without access to water sources.

The impacts of these and other introduced stream species in Hawaiʻi are needed to design the best management and the control strategies. This is partially due to the unique stream ecosystems found in Hawaiʻi and the unclear roles and functions of introduced species, which may exhibit differential responses to in-stream environmental conditions influenced by natural and anthropogenic factors. Few studies have examined introduced stream species in Hawaiʻi, and only one study encompassed multiple islands (E.g., Brasher et al. 2006), however no studies have investigated introduced species across all islands. Investigating introduced species use of in-stream environments and spatial distributions, including the associated landscape factors. This information would guide future management strategies as well as key future studies on the impacts to native species and ecosystems. The protection and conservation of stream ecosystems, particularly the protection of native stream biodiversity, is exceptionally important as human development and the related anthropogenic disturbances continue to expand throughout the Hawaiian Islands.

1.1.5 Landscape perspective of stream ecosystems

Hawaiʻi's tropical island ecosystems were evaluated from a landscape perspective to describe natural (e.g., topography, climate) and anthropogenic influences (e.g., urbanization, agriculture) on stream environments that support Hawaiian stream fauna across the state (Crawford et al. 2016). This type of landscape-scale approach has been increasingly applied to freshwater systems to evaluate the relative importance of landscape features to local biodiversity and to predict local biodiversity in areas where biological information is not available (See Tingley 2017 for example in Hawaiʻi; see Townsend et al. 2003, McNyset 2005, Oakes et al. 2005, Buisson et al. 2008, Wang et al. 2011, Maloney et al. 2013, Daniel et al. 2015, Cheek et al. 2016, Cooper et al. 2016 for examples in continental U.S.). One critical reason to adopt this landscape perspective on stream assessment is because the complexity in which stream environmental characteristics and the associated biological communities are influenced by stream network connectivity and their surroundings at multiple spatial scales (Schlosser 1991, Allan et al. 1997, Fausch et al. 2002, Townsend et al. 2003, Allan 2004), including (from largest to smallest): basins, catchments, sub-catchments, reaches, channel units (e.g., riffles and pools), and microhabitats (e.g., substrate, temperature, woody debris; Frissell et al. 1986, Townsend & Hildrew 1994, Ward & Palmer 1994, Pahl-Wostl 1998, Montgomery 1999, Habersack 2000, Wiens 2002, Allan 2004, Fausch et al. 2002). In this spatially-nested stream ecosystem, large scale factors (e.g., climate, geology, topography, land cover) influence the hydrological and geomorphic processes that control intermediate scale levels (i.e., reaches), which in turn affect the variety and distribution of in-stream environments at small scales (i.e., channel units and microhabitat; Frissell et al. 1986, Montgomery 1999, Fausch et al. 2002, Allan 2004). A better understanding of species and their use of stream environments at various spatial scales will allow us to describe the distribution of introduced species in Hawaiʻi and predict their potential distributions.

Species-environmental associations have numerous implications for the advancement of stream ecology and management, for example identifying environmental controls on community composition, the most effective scale for stream restoration, and the likelihood of establishment and spread of introduced species (Poff 1997). Additionally, species-environmental associations allow for the prediction of species distributions in locations where surveys have not been conducted. For example, species distribution models (SDMs) uses empirical data relating field observations of location data to landscape environmental predictor variables, based on statistically or theoretically derived response (Guisan & Zimmermann 2000). Ideal environmental predictors reflect species response to physiological limitations, disturbances, and resources (Guisan & Thuiller 2005). These modeling approaches have been applied to describe the freshwater species distributions in large temperate continental regions. Similarly, SDM has been applied to describe the range of native vegetation in Hawaiʻi (Fortini et al. 2013), but has not been applied to the freshwater species.

1.2 Objectives

The research proposed here utilized stream survey records, obtained from the State of Hawaiʻi's Department of Land and Natural Resources (DLNR), Division of Aquatic Resources (DAR), to investigate the in-stream environmental associations and distributions of introduced species in Hawaiian streams. In-stream environments of introduced species was evaluated with in-stream environmental attributes measured in stream surveys (Chapter One). Further, landscape associations of introduced species was evaluated with natural and anthropogenic landscape factors that were summarized at multiple spatial catchments (Chapter Two). The suitability of stream reach (i.e., segments of stream channels) for various introduced species was modeled using landscape-scale environmental factors (Chapter Three). Results from this research served to fill an important gap in scientific understanding of the environmental characteristics that support introduced species in Hawaiian streams and by providing resource managers with information to guide introduced species control and native species conservation.

1.3 Study area

This study proposes to evaluate streams (both perennial and intermittent) and their respective drainage basins throughout the five main Hawaiian Islands including Hawaiʻi, Maui, Molokaʻi, Oʻahu, and Kauaʻi. Geological age of the islands increases from the southeast (Hawaiʻi) to the northwest (Kauaʻi), and maximum elevation generally decreases with geological age (Figure 1.1). In general, mild temperatures, cool and persistent northeasterly trade winds, a rainy season from October through April, and a dry season from May through September characterize the climate of the Hawaiian Islands (Figure 1.2; Blumenstock & Price 1967, Sanderson 1993).

The main Hawaiian Islands can be divided into two primary physiographic zones, windward and leeward. Windward areas, the north-eastern sides of islands, are generally receive the most precipitation due to persistent northeasterly trade winds and the resulting orographic rainfall (Sanderson 1993). Leeward areas, the south-western sides of islands, are generally dry areas due to the rain-shadow effect (Giambelluca et al. 1986). Most streams originate in the mountainous interiors of islands and end at the coast where they empty into the ocean. Perennial streams, flowing continuously throughout the year, are common in areas that have significant rainfall and groundwater discharge (Oki 2004), and are primarily located in windward areas. Intermittent streams, where sections or the entire stream occasionally run dry, are frequently located in leeward areas, where significant rainfall and groundwater discharge are less common (Oki 2004; see Figure 1.3 for a spatial classification of perennial and intermittent streams).

1.4 Study data

The biological stream surveys used in this study were collected by DAR through different monitoring programs and were therefore classified as three different datasets: (1) abundance; (2) presence-absence; and (3) survey effort. These datasets were evaluated for standardization and reliability via communication with DAR biologist Glenn Higashi, who conducted most of these surveys. All datasets span the main five Hawaiian Islands including Hawaiʻi, Maui, Molokaʻi, Oʻahu, and Kauaʻi (Figures 1.4 – 1.8; with the exception of no presence-absence surveys conducted on the island of Molokaʻi). Surveys were primarily conducted in streams classified as perennial by the National Hydrography Dataset (NHD), although some were conducted on streams classified as intermittent. Note that stream hydrological classification varies based on organization, and therefore any difference between perennial and intermittent should be interpreted with caution.

(1) Abundance dataset

The abundance dataset included abundance records of introduced taxa using a standardized point quadrat visual survey method (Higashi & Nishimoto, 2007) collected by DAR during 1989 - 2009 (Table 1.1), which comprised a total of 1,984 surveys with 42 introduced taxa (Table 1.2). This survey method recorded visual counts of aquatic biota and in-stream environmental attributes at discrete points in a stream by a stationary observer. Individual surveys detailed information for a one-meter by one-meter quadrat and the corresponding water column, for a duration spanning three to seven minutes. These surveys were typically conducted at equal-distance intervals along the longitudinal axis of the stream, while the lateral location within the stream channel was determined by a combination of random and non-random methods.

Nearly all 1,984 surveys documented in-stream environmental attributes but not all surveys had a complete set of surveyed attributes. The in-stream attributes recorded in the abundance dataset included channel unit (*n*=1,959), substrate type (*n*=1,904), depth (*n*=1,844), temperature (*n*=1,353), dissolved oxygen (DO; *n*=224), specific conductance (*n*=224), pH (*n*=223), and turbidity (*n*=61). See Table 1.3 for the number of attributes recorded per taxa occurrence. Channel unit was classified as cascade, chute, riffle, run, pool, side pool, or plunge pool (Higashi & Nishimoto 2007; see Table 1.4 for channel unit definitions). Substrate was described as percent detritus, sediment, sand, gravel, cobble, boulder, and bedrock (Higashi & Nishimoto 2007; see Table 1.5 for substrate definitions).

(2) Presence-absence dataset

The presence-absence dataset included presence-absence records of introduced taxa from four similar visual survey methods collected by DAR from 1960 - 1969 and 2008 - 2014 (Table 1.6), including DAR biological assessment, DAR habitat assessment, DAR monitoring surveys, and Hawaiʻi Department of Fish and Game (HDFG) surveys (Table 1.7). This dataset included records for 466 surveys and 41 taxa (Table 1.8). The four presence-absence survey methods recorded visual presence of aquatic biota and in-stream environmental attributes along a 50 to 100 meter longitudinal section of stream channel by an observer moving upstream.

In-stream environmental attributes were recorded in 227 of the 466 surveys, and similar to the abundance dataset, not all surveys included a complete set of attributes. The attributes in this dataset included channel unit (*n*=117), modified status (*n*=171), substrate type (*n*=11), depth (*n*=31), temperature (*n*=149), DO (*n*=103), pH (*n*=146), and specific conductance (*n*=105). See Table 1.9 for the number of attributes per taxa. Channel unit was classified as riffle, run, cascade, pool, plunge pool, side pool or a combination of multiple channel units, e.g., "riffle-run". Records with such combinations were the result of a different survey method from abundance dataset, which include 50 – 100 meter longitudinal lengths of stream channels. When a combination of multiple channel units were recorded for a survey, the channel unit attribute were excluded in analyses as these surveys did not exhibit the appropriate precision to investigate species-environmental associations. The "modified status" attribute described the presence of channel alterations to the survey area and was classified as natural, modified, or earthen.

(3) Survey effort dataset

The survey effort dataset included information of abundance stream surveys during 1989-2010 (Table 1.10), which comprised a total of 7,964 surveys. Records in this dataset included spatial location, date, and a general classification of the biota observed in the study, with the following classifications: endemic, introduced, endemic and introduced, or no species observed. The purpose of this dataset in this study was to supplement the abundance dataset, so that we could describe those surveys without introduced species.

Chapter One Tables

Table 1.1. Distribution of surveys from the abundance dataset, summarized by year and island from 1989 to 2009.

Year	Hawai'i	Kaua'i	Maui	Moloka'i	O'ahu	Year Total
1989	1	-	-	-	-	1
1990	58	-	-	-	-	58
1991	50	-	-	12	-	62
1992	135	51	-	-	-	186
1993	36	59	-	-	-	95
1994	28	26	7	-	-	61
1995	56	-	8	-	-	64
1996	18	-	-	-	-	18
2000	-	1	-	-	110	111
2001	-	-	-	94	-	94
2002	-	39	86	97	231	453
2003	69	35	5	-	54	163
2004	141	29	11	-	5	186
2005	47	-	72	2	73	194
2006	58	22	-	-	-	80
2007	-	-	45	-	-	45
2008	-	-	64	-	-	64
2009	4	-	32	-	12	48
Island Total	701	262	330	205	485	

Table 1.2. Biological information from the abundance dataset. The total number of unique survey and total abundance, summarized by taxonomic rank (TR), type, and island. Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	Common Name	TR	Type	Total number of unique survey occurrence (Total abundance)					
				All islands	Hawai'i	Kaua'i	Maui	Moloka'i	O'ahu
Ancistrus cf. temminckii	Bristle-nosed Catfish	Sp	fish	3 (3)	-	-	-	-	3 (3)
Archocentrus nigrofasciatus	Convict Cichlid	Sp	fish	4 (4)	-	-	-	-	4 (4)
Bufo marinus	Cane Toad	Sp	amph.	48 (1145)	10 (56)	25 (842)	13 (247)	-	-
Carassius auratus	Goldfish	Sp	fish	5 (16)	-	-	5 (16)	-	-
Chironomid spp.	Midges	F	insect	1 (1)	-	-	1 (1)	-	-
Clarias fuscus	Chinese Catfish	Sp	fish	1 (1)	-	-	-	-	1 (1)
Corbicula fluminea	Asian Clam	Sp	mollusk	14 (26)	-	7 (18)	-	-	7 (8)
Dugesia spp.	Flatworms	G	other	4 (144)	-	-	-	-	4 (144)
Enallagma civile	Familiar Bluet	Sp	insect	3 (3)	2	-	-	-	1 (1)
Gambusia affinis	Western Mosquitofish	Sp	fish	59 (437)	38 (329)	1 (6)	8 (61)	-	12 (41)
Helisoma spp.	Helisoma Snails	G	mollusk	5 (5)	-	-	-	-	5 (5)
Hemichromis fasciatus	Banded Jewelfish	Sp	fish	4 (6)	-	-	-	-	4 (6)
Hypostomus watwata	Armored Catfish	Sp	fish	8 (18)	-	-	-	-	8 (18)
Isopod spp.	Isopods	O	other	3 (217)	-	3 (217)	-	-	-
Limia vittata	Cuban Limia	Sp	fish	3 (28)	-	-	-	-	3 (28)
Lymnaeid spp.	Lymnaeid Snails	F	mollusk	7 (44)	3 (14)	-	1 (1)	1 (25)	2 (4)
Macrobrachium lar	Tahitian Prawn	Sp	crust.	1247 (3267)	540 (1840)	136 (263)	175 (357)	206 (458)	189 (347)
Melania spp.	Melania Snails	G	mollusk	47 (49)	-	1 (1)	-	2 (3)	44 (45)
Melanoides tuberculate	Red-rimmed Melania	Sp	mollusk	46 (2181)	8 (20)	1 (1)	4 (7)	-	33 (2153)
Micropterus dolomieu	Smallmouth Bass	Sp	fish	4 (4)	-	4 (4)	-	-	-
Micropterus salmoides	Largemouth Bass	Sp	fish	2 (5)	-	2 (5)	-	-	-
Misgurnus anguillicaudatus	Pond Loach	Sp	fish	15 (30)	8 (18)	-	-	-	7 (12)
Oreochromis mossambicus	Mozambique Tilapia	Sp	fish	1 (12)	-	1 (12)	-	-	-
Palea steindachneri	Watter-Necked Softshell Turtle	Sp	reptile	1 (1)	-	-	-	-	1 (1)
Physid spp.	Bladder Snails	F	mollusk	29 (171)	3 (5)	-	26 (166)	-	-
Plumatella repens	Moss Animal	Sp	other	1 (1)	1 (1)	-	-	-	-
Poecilia latipinna	Sailfin Molly	Sp	fish	1 (2)	-	-	1 (2)	-	-
Poecilia reticulata	Guppy	Sp	fish	155 (1211)	35 (400)	12 (107)	66 (544)	-	42 (160)
Poecilia sphenops	Common Molly	Sp	fish	44 (282)	1 (1)	5 (62)	1 (1)	-	37 (218)
Poeciliidae spp.	Poeciliid	F	fish	133 (1735)	35 (172)	32 (371)	47 (1116)	-	19 (76)

Table 1.2 continued. Biological information from the abundance dataset. The total number of unique survey and total abundance, summarized by taxonomic rank (TR), type, and island. Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	**Common Name**	**TR**	**Type**	**Total number of unique survey occurrence (Total abundance)**					
				All islands	**Hawai'i**	**Kaua'i**	**Maui**	**Moloka'i**	**O'ahu**
Pomacea canaliculata	Channeled Apple Snail	Sp	mollusk	7 (16)	-	-	1 (3)	-	6 (13)
Procambarus clarkii	Red Swamp Crayfish	Sp	crust.	54 (192)	44 (174)	-	10 (18)	-	-
Rana catesbiana	American Bullfrog	Sp	amph.	20 (62)	6 (8)	5	5 (34)	-	4 (4)
Rana rugosa	Japanese Wrinkled Frog	Sp	amph.	17 (54)	-	11 (37)	5 (15)	-	1 (2)
Ranid spp.	True Frogs	F	amph.	21 (404)	4 (353)	6 (29)	9 (19)	-	2 (3)
Sarotherodon melanotheron	Blackchin Tilapia	Sp	fish	4 (103)	-	-	-	-	4 (103)
Tarebia granifera	Quilted Melania Snail	Sp	mollusk	27 (212)	-	14 (174)	-	-	13 (38)
Thiara spp.	Thirad Snails	G	mollusk	1 (2)	-	-	1 (2)	-	-
Tilapiini (*Cichlidae*) spp.	Tilapia	-	fish	9 (278)	-	9 (278)	-	-	-
Tilapia zilli	Redbelly Tilapia	Sp	fish	1 (1)	-	1 (1)	-	-	-
Tramea abdominalis	Vermillion Saddlebags	Sp	insect	1 (1)	-	-	-	-	1 (1)
Xiphophorus helleri	Green Swordtail	Sp	fish	322 (1985)	67 (390)	31 (236)	19 (107)	-	205 (1252)

Table 1.3. In-stream environmental attributes from the abundance dataset, summarized by taxonomic rank (TR), type, total abundance (TA), total number of unique survey occurrences (Surveys), and the number of various habitat attributes associated with each taxon occurrence. Habitat attributes include: channel unit (CU), substrate (Sub), depth (Dep), temperature (Temp), dissolved oxygen (DO), pH, turbidity (Turb), and specific conductance (SC). Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	**Common Name**	**TR**	**Type**	**TA**	**Surveys**	**Habitat Attributes**							
						CU	**Sub**	**Dep**	**Temp**	**DO**	**pH**	**Turb**	**SC**
Ancistrus cf. temminckii	Bristle-nosed Catfish	Sp	fish	3	3	3	3	3	-	-	-	-	-
Archocentrus nigrofasciatus	Convict Cichlid	Sp	fish	4	4	4	4	4	4	-	-	-	-
Bufo marinus	Cane Toad	Sp	amph.	1145	48	47	43	39	20	7	7	-	7
Carassius auratus	Goldfish	Sp	fish	16	5	4	4	4	4	-	-	-	-
Chironomid spp.	Midges	F	insect	1	1	1	-	1	1	1	1	-	1
Clarias fuscus	Chinese Catfish	Sp	fish	1	1	1	1	1	1	-	-	-	-
Corbicula fluminea	Asian Clam	Sp	mollusk	26	14	14	14	14	13	1	1	1	1
Dugesia spp.	Flatworms	G	other	144	4	4	4	4	4	-	-	-	-
Enallagma civile	Familiar Bluet	Sp	insect	3	3	3	3	3	3	-	-	-	-
Gambusia affinis	Western Mosquitofish	Sp	fish	437	59	57	57	50	33	7	7	-	7
Helisoma spp.	Helisoma Snails	G	mollusk	5	5	5	5	5	5	-	-	-	-
Hemichromis fasciatus	Banded Jewelfish	Sp	fish	6	4	4	4	4	4	-	-	-	-
Hypostomus watwata	Armored Catfish	Sp	fish	18	8	8	8	8	5	-	-	-	-
Isopod spp.	Isopods	O	other	217	3	3	2	2	-	-	-	-	-
Limia vittata	Cuban Limia	Sp	fish	28	3	3	3	3	1	-	-	-	-
Lymnaeid spp.	Lymnaeid Snails	F	mollusk	44	7	7	7	7	5	-	-	-	-
Macrobrachium lar	Tahitian Prawn	Sp	crust.	3267	1247	1230	1192	1140	773	109	108	29	109
Melania spp.	Melania Snails	G	mollusk	49	47	46	47	46	46	-	-	-	-
Melanoides tuberculate	Red-rimmed Melania	Sp	mollusk	2181	46	46	46	45	45	6	6	2	6
Micropterus dolomieu	Smallmouth Bass	Sp	fish	4	4	4	4	4	4	-	-	-	-
Micropterus salmoides	Largemouth Bass	Sp	fish	5	2	2	2	2	2	1	1	1	1
Misgurnus anguillicaudatus	Pond Loach	Sp	fish	30	15	14	14	15	8	-	-	-	-
Oreochromis mossambicus	Mozambique Tilapia	Sp	fish	12	1	1	-	-	-	-	-	-	-
Palea steindachneri	Wattle-Necked Softshell Turtle	Sp	reptile	1	1	1	1	1	-	-	-	-	-
Physid spp.	Bladder Snails	F	mollusk	171	29	28	28	28	25	9	9	5	9
Plumatella repens	Moss Animal	Sp	other	1	1	1	1	1	-	-	-	-	-

Table 1.3 continued In-stream environmental attributes from the abundance dataset, summarized by taxonomic rank (TR), type, total abundance (TA), total number of unique survey occurrences (Surveys), and the number of various habitat attributes associated with each taxon occurrence. Habitat attributes include: channel unit (CU), substrate (Sub), depth (Dep), temperature (Temp), dissolved oxygen (DO), pH, turbidity (Turb), and specific conductance (SC). Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	**Common Name**	**TR**	**Type**	**TA**	**Surveys**	**Habitat Attributes**							
						CU	**Sub**	**Dep**	**Temp**	**DO**	**pH**	**Turb**	**SC**
Poecilia latipinna	Sailfin Molly	Sp	fish	2	1	1	1	1	1	-	-	-	-
Poecilia reticulata	Guppy	Sp	fish	1211	155	152	152	150	126	49	49	14	49
Poecilia sphenops	Common Molly	Sp	fish	282	44	44	44	44	42	1	1	-	1
Poeciliidae spp.	Poeciliid	F	fish	1735	133	133	130	126	89	20	20	2	20
Pomacea canaliculata	Channeled Apple Snail	Sp	mollusk	16	7	7	7	7	7	-	-	-	-
Procambarus clarkii	Red Swamp Crayfish	Sp	crust.	192	54	54	52	54	38	18	18	4	18
Rana catesbiana	American Bullfrog	Sp	amph.	62	20	20	18	19	13	-	-	-	-
Rana rugosa	Japanese Wrinkled Frog	Sp	amph.	54	17	17	14	15	6	1	1	1	1
Ranid spp.	True Frogs	F	amph.	404	21	20	19	19	9	5	5	3	5
Sarotherodon melanotheron	Blackchin Tilapia	Sp	fish	103	4	4	4	4	4	-	-	-	-
Tarebia granifera	Quilted Melania Snail	Sp	mollusk	212	27	27	27	27	25	6	6	4	6
Thiara spp.	Thirad Snails	G	mollusk	2	1	-	-	-	-	-	-	-	-
Tilapiini (*Cichlidae*) spp.	Tilapia	-	fish	278	9	9	9	9	6	-	-	-	-
Tilapia zilli	Redbelly Tilapia	Sp	fish	1	1	1	1	1	1	-	-	-	-
Tramea abdominalis	Vermillion Saddlebags	Sp	insect	1	1	1	1	1	1	-	-	-	-
Xiphophorus helleri	Green Swordtail	Sp	fish	1985	322	321	317	314	277	41	41	4	41

Table 1.4. Channel unit descriptions used to characterize in-stream environments in the abundance dataset (Higashi & Nishimoto 2007).

Channel Unit	Depth (m)	Current (m/sec)	Turbulence
Pool	variable	< 0.2	no
Side Pool	< 0.5 usually	nil usually	no
Plunge Pool	< 2.0 usually	< 0.20	yes
Run	variable	0.20 - 0.75+	no
Riffle	< 0.5	> 0.75	yes
Cascade	~ 2.0 usually	> 2.0	much

Table 1.5. Substrate type descriptions used to characterize in-stream environments in the abundance and presence-absence datasets (Higashi & Nishimoto 2007).

Size Category	Particle Diameter (mm)	Reference
Boulder	>256	head-size and larger
Cobble	64-256	fist-size
Gravel	2-64	thumb-size
Sand	0.062-2.000	sand-size
Silt	>0.062	smaller than pin head

Table 1.6. Distribution of surveys from the presence-absence dataset, summarized by year and island from 1960 to 2014.

Year	Hawai'i	Kaua'i	Maui	Moloka'i	O'ahu	Year Total
1960	-	-	-	-	4	4
1961	-	-	6	-	20	26
1962	-	-	1	-	1	2
1963	-	22	-	-	2	24
1964	-	4	-	-	-	4
1965	-	15	-	-	-	15
1966	2	8	-	-	-	10
1967	24	-	-	-	-	24
1968	11	-	-	-	-	11
1969	-	-	-	-	2	2
2008	-	-	-	-	60	60
2010	8	-	16	-	-	24
2011	20	-	24	-	10	54
2012	3	-	56	-	42	101
2013	-	54	31	-	8	93
2014	-	8	-	-	3	11
Island Total	68	111	134	0	152	

Table 1.7. Distribution of surveys from the presence-absence dataset, summarized by survey method and year from 1960 to 2014. The Hawai'i State Division of Aquatic Resources is abbreviated as DAR.

Year	DAR Biological Assessment	DAR Habitat Assessment	DAR Hybrid Rapid Monitoring Survey	Hawai'i Dept. of Fish and Game
1960	-	-	-	4
1961	-	-	-	26
1962	-	-	-	2
1963	-	-	-	24
1964	-	-	-	4
1965	-	-	-	15
1966	-	-	-	10
1967	-	-	-	24
1968	-	-	-	11
1969	-	-	-	2
2008	60	-	-	-
2010	7	-	17	-
2011	10	-	44	-
2012	1	33	67	-
2013	58	-	35	-
2014	8	-	3	-
Method Total	144	33	166	122

Table 1.8. Biological information from the presence-absence dataset. The total number of unique surveys summarized by taxonomic rank (TR), type, and island. Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	Common Name	TR	Type	Total number of unique survey occurrence					
				All islands	Hawaiʻi	Kauaʻi	Maui	Molokaʻi	Oʻahu
Ancistrus cf. temminckii	Bristle-nosed Catfish	Sp	fish	18	-	-	-	-	18
Archocentrus nigrofasciatus	Convict Cichlid	Sp	fish	4	-	2	-	-	2
Assiminea spp.	Assiminea Snails	G	mollusk	2	-	-	-	-	2
Bufo marinus	Cane Toad	Sp	amph.	16	-	10	-	-	6
Carassius auratus	Goldfish	Sp	fish	3	-	-	-	-	3
Cichla ocellaris	Butterfly Peacock Bass	Sp	fish	1	-	1	-	-	-
Clarias fuscus	Chinese Catfish	Sp	fish	1	-	-	-	-	1
Corbicula fluminea	Asian Clam	Sp	mollusk	5	-	5	-	-	-
Cyprinus carpio	Common Carp	Sp	fish	3	-	3	-	-	-
Gambusia affinis	Western Mosquitofish	Sp	fish	52	2	37	-	-	13
Isopod spp.	Isopods	O	other	2	2	-	-	-	-
Lepomis macrochirus	Bluegill	Sp	fish	2	-	2	-	-	-
Lepomis spp.	Sunfishes	G	fish	5	-	4	-	-	1
Limia vittata	Cuban Limia (Molly)	Sp	fish	1	-	-	-	-	1
Lymnaeid spp.	Lymnaeid Snails	F	mollusk	20	1	13	5	-	1
Macrobrachium lar	Tahitian Prawn	Sp	crust.	207	38	14	83	-	72
Melania spp.	Melania Snails	G	mollusk	13	1	4	3	-	5
Melanoides tuberculate	Red-rimmed Melania	Sp	mollusk	1	1	-	-	-	-
Micropterus dolomieu	Smallmouth Bass	Sp	fish	22	-	20	-	-	2
Micropterus salmoides	Largemouth Bass	Sp	fish	7	-	6	-	-	1
Misgurnus anguillicaudatus	Pond Loach	Sp	fish	6	-	-	-	-	6
Neocaridina denticulata	Cherry Shrimp	Sp	crust.	3	-	-	-	-	3
Oncorhynchus mykiss	Rainbow Trout	Sp	fish	5	-	2	1	-	2
Oreochromis mossambicus	Mozambique Tilapia	Sp	fish	7	1	6	-	-	-
Parachromis managuensis	Jaguar Guapote Cichlid	Sp	fish	1	-	-	-	-	1
Pelodiscus sinensis	Chinese Softshell Turtle	Sp	reptile	1	-	-	-	-	1
Physid spp.	Bladder Snails	F	mollusk	18	-	-	11	-	7
Poecilia reticulata	Guppy	Sp	fish	121	2	14	28	-	77
Poecilia sphenops	Common Molly	Sp	fish	8	-	-	-	-	8
Poeciliidae spp.	Poeciliid	F	fish	56	28	10	4	-	14
Pomacea spp.	Apple Snails	G	mollusk	3	-	3	-	-	-
Procambarus clarkii	Red Swamp Crayfish	Sp	crust.	50	13	20	-	-	17
Rana catesbiana	American Bullfrog	Sp	amph.	13	-	8	3	-	2

Table 1.8 continued. Biological information from the presence-absence dataset. The total number of unique surveys summarized by taxonomic rank (TR), type, and island. Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	**Common Name**	**TR**	**Type**	**Total number of unique survey occurrence**					
				All islands	**Hawaiʻi**	**Kauaʻi**	**Maui**	**Molokaʻi**	**Oʻahu**
Rana rugosa	Japanese Wrinkled Frog	Sp	amph.	29	-	-	26	-	3
Ranid spp.	True Frogs	F	amph.	4	1	-	2	-	1
Tarebia granifera	Quilted Melania Snail	S	mollusk	1	-	-	-	-	1
Thiara spp.	Thirad Snails	G	mollusk	8	-	4	-	-	4
Tilapiini (Cichlidae) spp.	Tilapia	-	fish	24	-	12	-	-	12
Valamugil engeli	Kanda Mullet	Sp	fish	1	-	-	-	-	1
Xiphophorus helleri	Green Swordtail	Sp	fish	137	2	42	-	-	93
Xiphophorus maculatus	Southern Platyfish	Sp	fish	2	-	-	-	-	2

Table 1.9. In-stream environmental attributes from the presence-absence dataset, summarized by taxonomic rank (TR), type, total number of unique survey occurrences (Surveys), and the number of survey attributes associated with each taxon. In-stream attributes include: channel unit (CU), modified status (Mod), substrate (Sub), depth (Dep), temperature (Temp), dissolved oxygen (DO), pH, and specific conductance (SC). Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	**Common Name**	**TR**	**Type**	**Surveys**	**Habitat Attributes**							
					CU	**Mod**	**Sub**	**Dep**	**Temp**	**DO**	**pH**	**SC**
Ancistrus cf. temminckii	Bristle-nosed Catfish	Sp	fish	9	9	9	-	-	3	3	3	3
Archocentrus nigrofasciatus	Convict Cichlid	Sp	fish	4	4	4	-	-	2	2	2	2
Assiminea spp.	Assiminea Snails	G	mollusk	2	-	-	-	-	-	-	-	-
Bufo marinus	Cane Toad	Sp	amph.	16	14	14	-	-	10	10	10	10
Carassius auratus	Goldfish	Sp	fish	3	-	-	-	-	-	-	-	-
Cichla ocellaris	Butterfly Peacock Bass	Sp	fish	1	-	1	-	-	-	-	-	-
Clarias fuscus	Chinese Catfish	Sp	fish	1	-	-	-	-	-	-	-	-
Corbicula fluminea	Asian Clam	Sp	mollusk	5	2	5	-	-	2	2	2	2
Cyprinus carpio	Common Carp	Sp	fish	3	1	1	-	-	1	1	1	1
Gambusia affinis	Western Mosquitofish	Sp	fish	52	27	43	-	-	33	31	32	31
Isopod spp.	Isopods	O	other	2	-	-	-	-	2	-	2	-
Lepomis macrochirus	Bluegill	Sp	fish	2	1	1	-	-	1	1	1	1
Lepomis spp.	Sunfishes	G	fish	5	-	-	-	-	-	-	-	-
Limia vittata	Cuban Limia	Sp	fish	1	-	1	-	-	1	1	1	1
Lymnaeid spp.	Lymnaeid Snails	F	mollusk	20	-	-	-	-	4	-	4	-
Macrobrachium lar	Tahitian Prawn	Sp	crust.	207	32	67	-	18	29	18	29	21
Melania spp.	Melania Snails	G	mollusk	13	-	-	-	-	4	-	4	-
Melanoides tuberculate	Red-rimmed Melania	Sp	mollusk	1	-	-	-	-	-	-	-	-
Micropterus dolomieu	Smallmouth Bass	Sp	fish	22	2	2	-	-	2	2	2	2
Micropterus salmoides	Largemouth Bass	Sp	fish	7	2	2	-	-	2	2	2	2
Misgurnus anguillicaudatus	Pond Loach	Sp	fish	6	-	1	-	-	1	-	1	1
Neocaridina denticulata	Cherry Shrimp	Sp	crust.	3	-	1	-	-	-	-	-	-
Oncorhynchus mykiss	Rainbow Trout	Sp	fish	5	2	2	-	-	3	2	3	2
Oreochromis mossambicus	Mozambique Tilapia	Sp	fish	7	-	-	-	-	1	-	1	-
Parachromis managuensis	Jaguar Guapote Cichlid	Sp	fish	1	1	1	-	-	-	-	-	-

Table 1.9 continued. In-stream environmental attributes from the presence-absence dataset, summarized by taxonomic rank (TR), type, total number of unique survey occurrences (Surveys), and the number of survey attributes associated with each taxon. In-stream attributes include: channel unit (CU), modified status (Mod), substrate (Sub), depth (Dep), temperature (Temp), dissolved oxygen (DO), pH, and specific conductance (SC). Taxonomic rank is listed as species (Sp), genus (G), family (F), and order (O). Type serves as a general biological classification.

Scientific Name	**Common Name**	**TR**	**Type**	**Surveys**	**Habitat Attributes**							
					CU	**Mod**	**Sub**	**Dep**	**Temp**	**DO**	**pH**	**SC**
Pelodiscus sinensis	Chinese Softshell Turtle	Sp	reptile	1	-	1	-	-	1	1	1	1
Physid spp.	Bladder Snails	F	mollusk	18	-	-	-	-	-	-	-	-
Poecilia reticulata	Guppy	Sp	fish	121	31	49	5	5	38	34	38	38
Poecilia sphenops	Common Molly	Sp	fish	8	6	7	-	4	1	1	1	1
Poeciliidae spp.	Poeciliid	F	fish	56	17	15	5	5	44	17	42	17
Pomacea spp.	Apple Snails	G	mollusk	3	1	3	-	-	1	1	1	1
Procambarus clarkii	Red Swamp Crayfish	Sp	crust.	50	13	14	-	-	25	12	23	12
Rana catesbiana	American Bullfrog	Sp	amph.	13	8	10	-	-	7	7	7	7
Rana rugosa	Japanese Wrinkled Frog	Sp	amph.	29	4	9	-	-	7	7	7	7
Ranid spp.	True Frogs	F	amph.	4	-	-	-	-	-	-	-	-
Tarebia granifera	Quilted Melania Snail	Sp	mollusk	1	-	-	-	-	-	-	-	-
Thiara spp.	Thirad Snails	G	mollusk	8	4	8	-	-	7	7	7	7
Tilapiini (*Cichlidae*) spp.	Tilapia	-	fish	24	20	22	-	2	21	21	21	21
Valamugil engeli	Kanda Mullet	Sp	fish	1	1	1	-	-	1	1	1	1
Xiphophorus helleri	Green Swordtail	Sp	fish	137	48	72	8	16	48	42	48	44
Xiphophorus maculatus	Southern Platyfish	Sp	fish	2	2	2	-	-	2	2	2	2

Table 1.10. Distribution of surveys from the survey effort dataset, detailing the sampling effort of DLNR abundance stream surveys, summarized by year and island from 1989 to 2010.

Year	Hawai'i	Kaua'i	Maui	Moloka'i	O'ahu	Year Total
1989	41	-	-	-	-	41
1990	510	-	-	-	-	510
1991	137	-	-	328	-	465
1992	432	302	-	-	-	734
1993	149	369	-	-	-	518
1994	172	233	321	-	-	726
1995	181	-	139	-	-	320
1996	25	-	-	-	-	25
2000	-	-	-	-	324	324
2001	-	-	-	299	186	485
2002	-	186	321	257	582	1346
2003	249	78	113	-	126	566
2004	336	118	151	-	28	633
2005	72	-	212	35	135	454
2006	135	46	-	-	-	181
2007	-	-	87	-	-	87
2008	1	-	304	-	-	305
2009	21	-	186	-	31	238
2010	1	-	-	-	5	6
Island Total	2462	1332	1834	919	1417	

Chapter One Figures

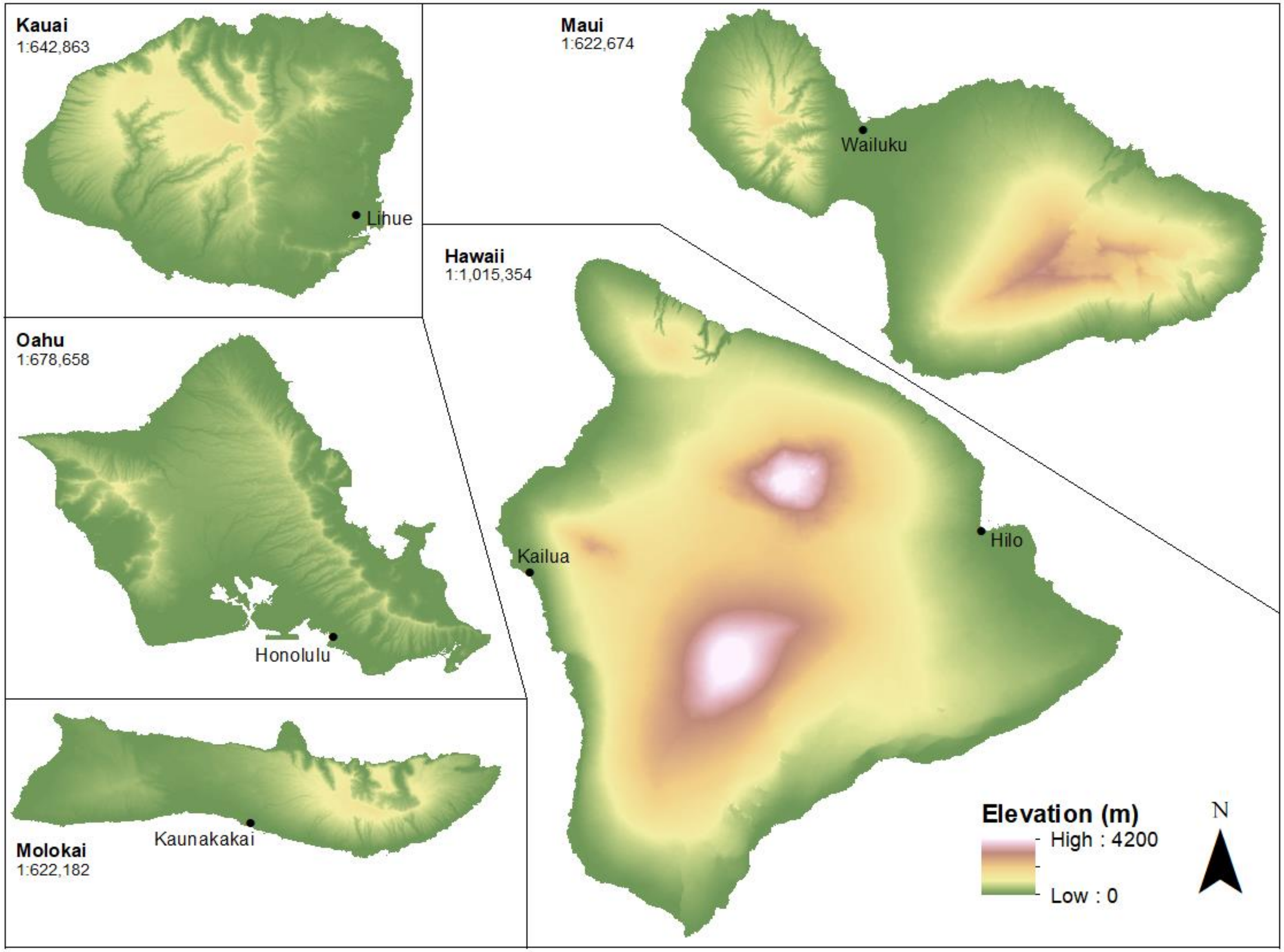


Figure 1.1. Elevation map of the five main Hawaiian Islands.

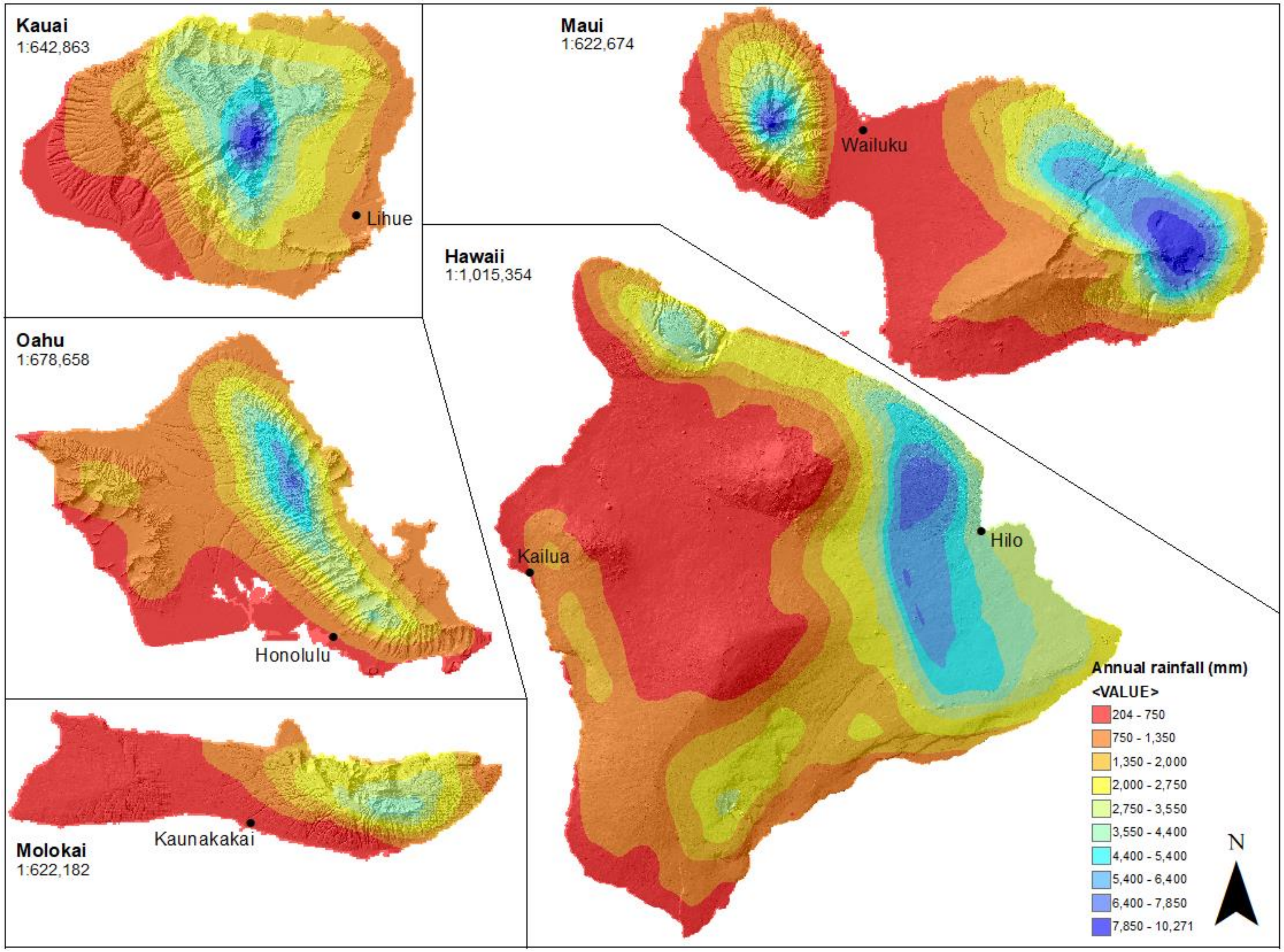


Figure 1.2. Mean annual rainfall map of the five main Hawaiian Islands (Giambelluca et al. 2013).

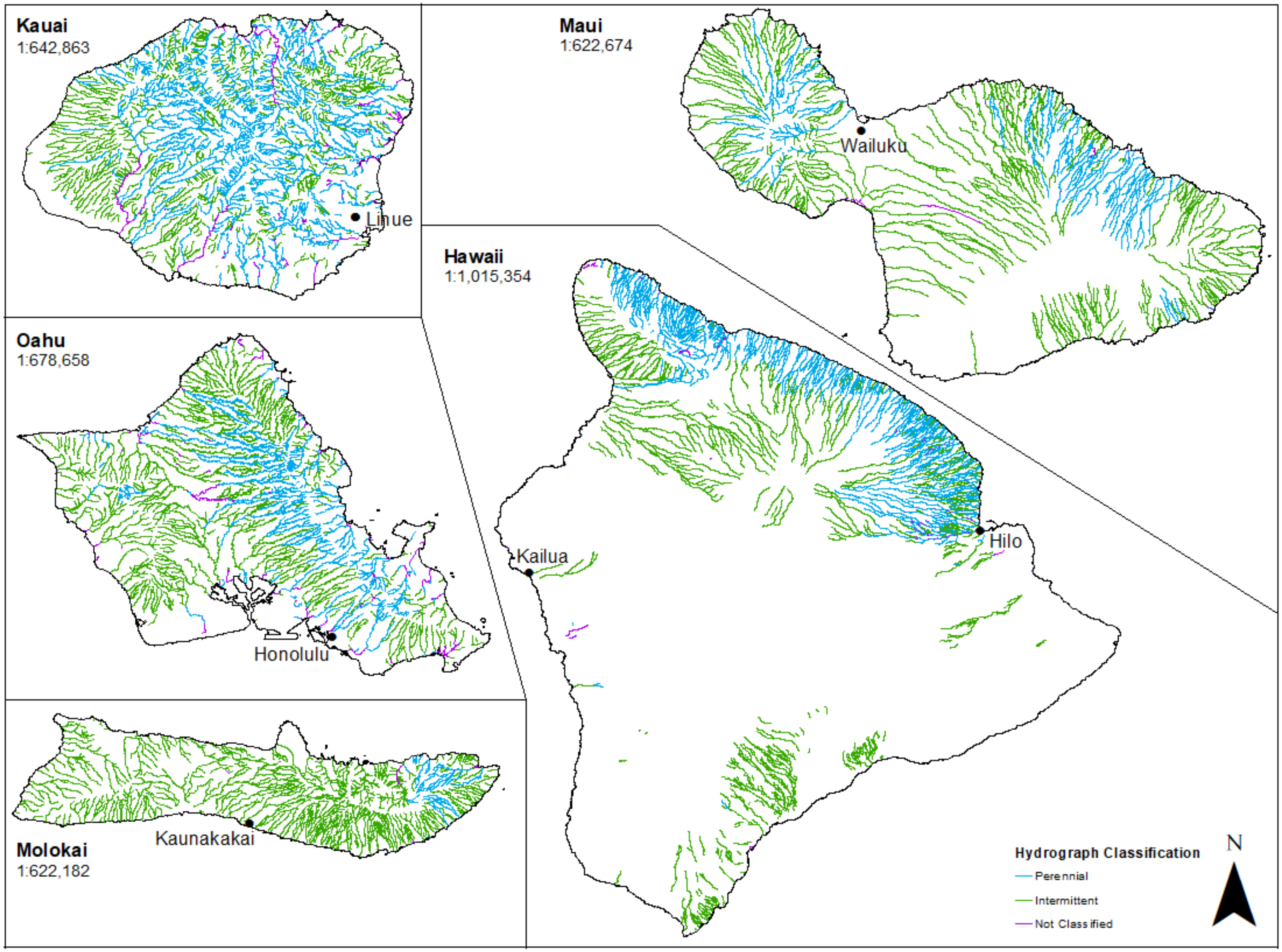


Figure 1.3. Map of stream hydrograph classfications for the five main Hawaiian Islands, streams are classified as perennial, intermittent, or not classified.

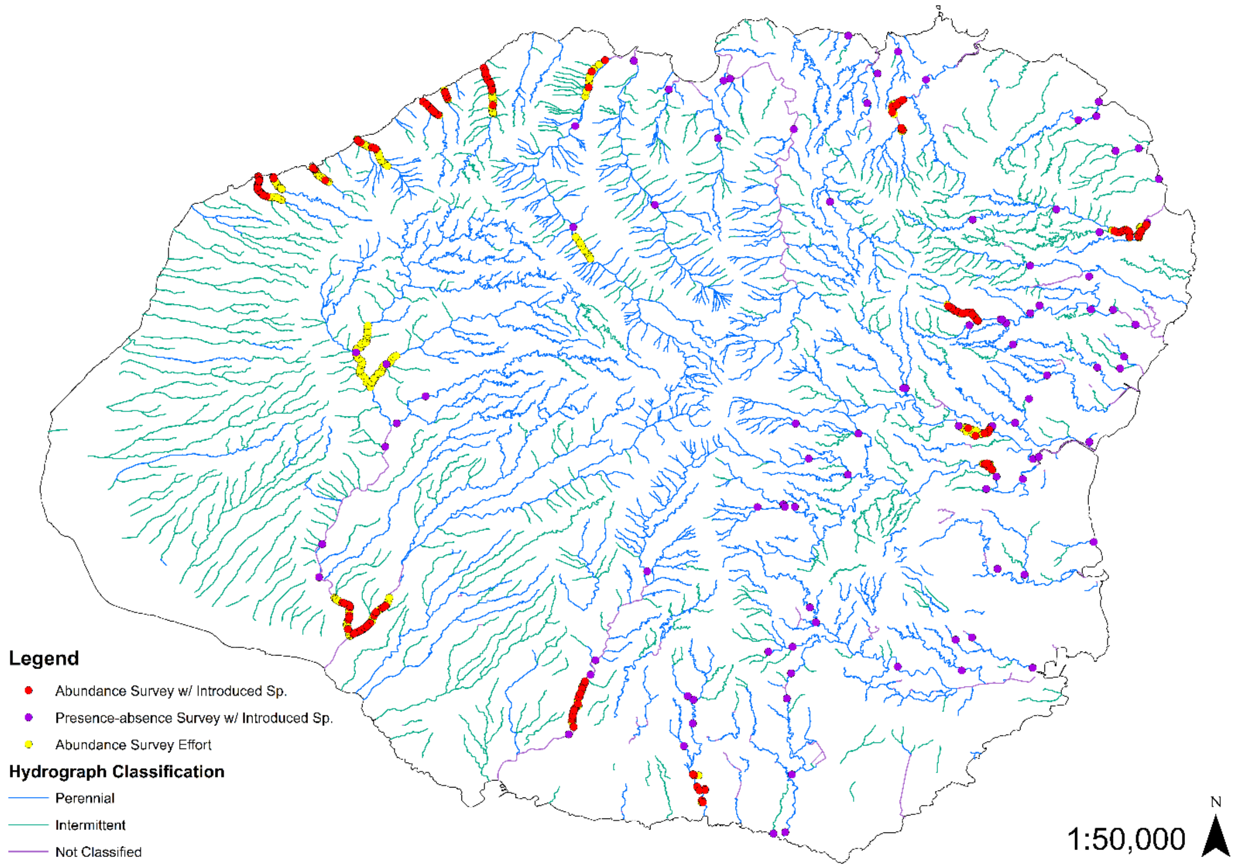


Figure 1.4. Map of biological surveys on the island of Kauaʻi. Red points represent abundance surveys where introduced species were observed (information from the abundance dataset), purple points represent presence-absence surveys where introduced species were observed (information from the presence-absence dataset), yellow points represent abundance surveys where introduced species were not observed (information from the survey effort dataset). Stream lines are colored by the hydrograph classification of the reach, with perennial streams in blue, intermittent streams in green, and non-classified streams in purple.

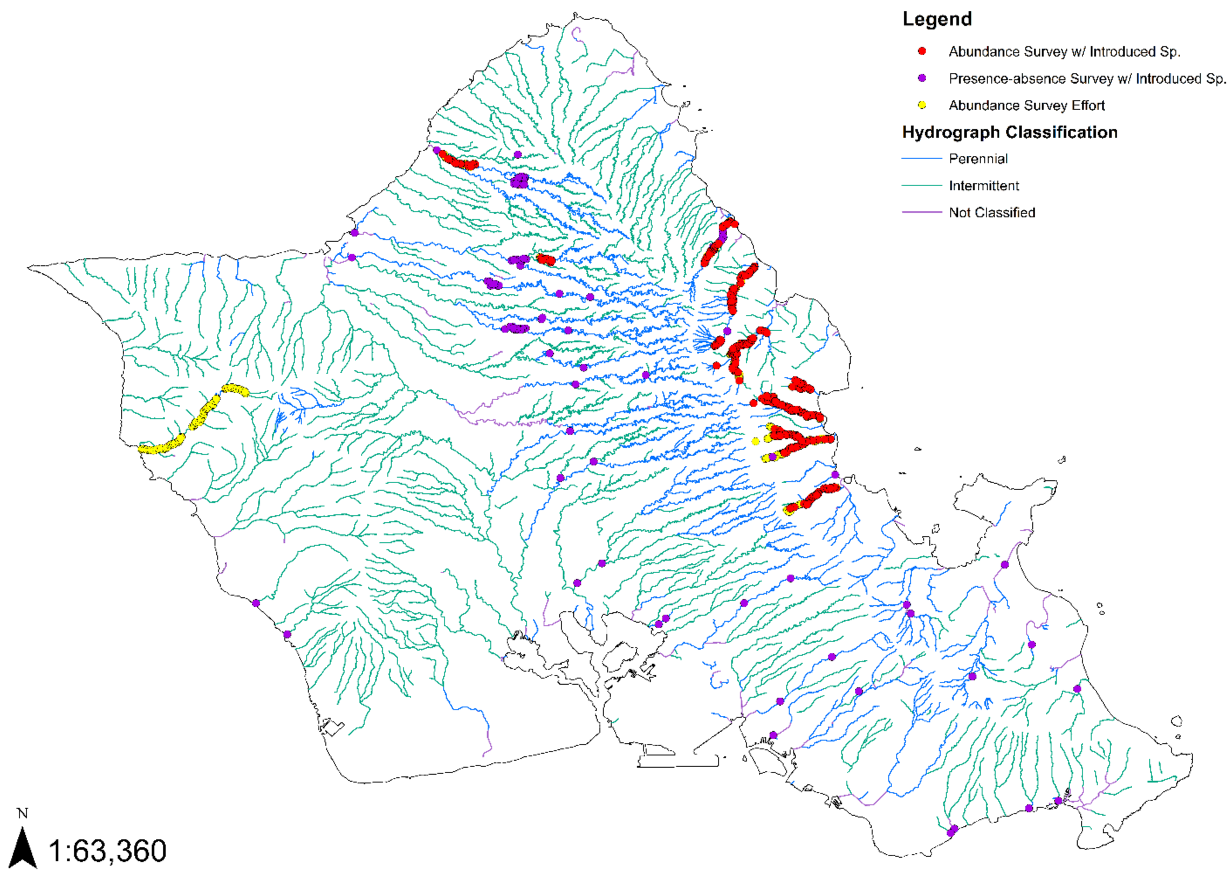


Figure 1.5. Map of biological surveys on the island of Oʻahu. Red points represent abundance surveys where introduced species were observed (information from the abundance dataset), purple points represent presence-absence surveys where introduced species were observed (information from the presence-absence dataset), yellow points represent abundance surveys where introduced species were not observed (information from the survey effort dataset). Stream lines are colored by the hydrograph classification of the reach, with perennial streams in blue, intermittent streams in green, and non-classified streams in purple.

Figure 1.6. Map of biological surveys on the island of Molokaʻi. Red points represent abundance surveys where introduced species were observed (information from the abundance dataset), purple points represent presence-absence surveys where introduced species were observed (information from the presence-absence dataset), yellow points represent abundance surveys where introduced species were not observed (information from the survey effort dataset). Stream lines are colored by the hydrograph classification of the reach, with perennial streams in blue, intermittent streams in green, and non-classified streams in purple.

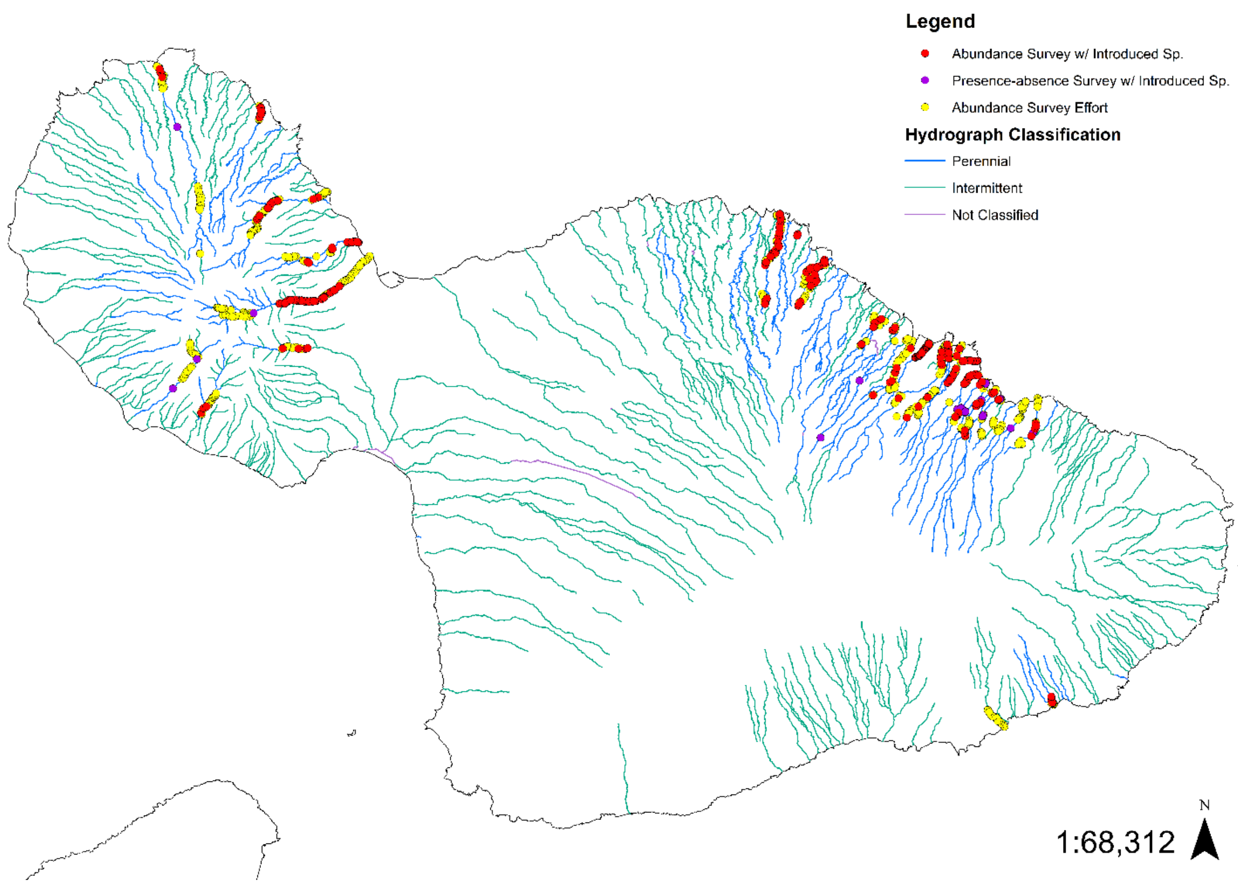


Figure 1.7. Map of biological surveys on the island of Maui. Red points represent abundance surveys where introduced species were observed (information from the abundance dataset), purple points represent presence-absence surveys where introduced species were observed (information from the presence-absence dataset), yellow points represent abundance surveys where introduced species were not observed (information from the survey effort dataset). Stream lines are colored by the hydrograph classification of the reach, with perennial streams in blue, intermittent streams in green, and non-classified streams in purple.

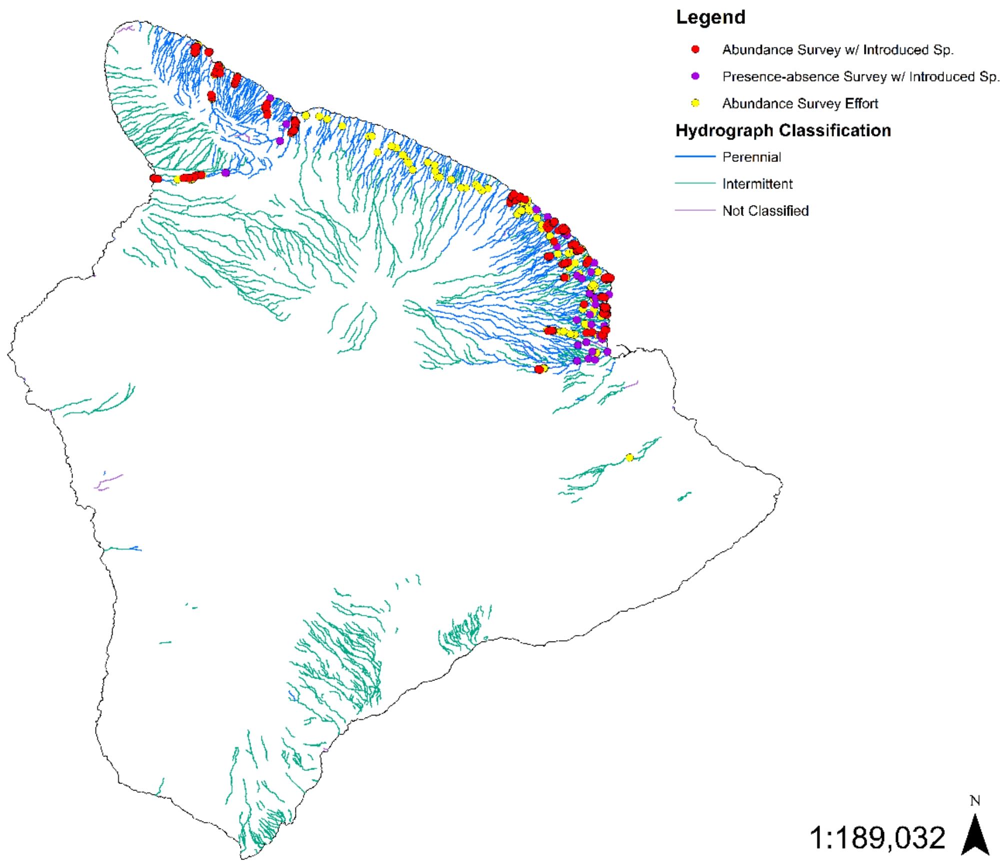


Figure 1.8. Map of biological surveys on the island of Hawaiʻi. Red points represent abundance surveys where introduced species were observed (information from the abundance dataset), purple points represent presence-absence surveys where introduced species were observed (information from the presence-absence dataset), yellow points represent abundance surveys where introduced species were not observed (information from the survey effort dataset). Stream lines are colored by the hydrograph classification of the reach, with perennial streams in blue, intermittent streams in green, and non-classified streams in purple.

Chapter Two – Characterizing introduced species associations with in-stream environmental attributes

2.1 Introduction

Variation in the structure of stream environments is a primary factor, along with the pool of species available for colonization, for influencing the abundance and diversity of stream biota (Hawkins et al. 1993). In-stream environmental attributes are defined by types of substrates, temperature, and dissolved oxygen in streams, and different characteristics of streamflow (e.g., velocity and depth). In-stream environmental attributes may directly limit species establishment by exceeding species physiological tolerances, such as high streamflow velocities, high or low water temperatures, and low dissolved oxygen concentrations. Additionally, in-stream environmental attributes indirectly limit species establishment by influencing community trophic dynamics and by altering levels of food resources, competition, and predation (Frissell et al. 1986). For example, interactions between sunlight, nutrients, and water velocity influence the type and amount of primary production, while interactions between water velocity and substrate size would likely influence predator-prey interactions. Previous studies often classified stream environments with a riffle-run-pool classification system (i.e., channel units), which aimed to describe areas of streams with similar bed topography, depth, and velocity patterns (Frissell et al. 1986).

Introduced freshwater species are often trophic and environmental generalists, which are better adapted to survive in a wide range of environmental conditions and can thus outcompete stress-intolerant and specialized native species (Brasher et al. 2006). Dense human populations have led to extensive impacts to stream environments resulting from urbanization and agriculture, which consequently create stream environmental conditions that favor of introduced species over native species (Brasher 2003, Brasher et al. 2006). In a comparison between developed and undeveloped sites among 22 streams across Kauaʻi, Oʻahu, and Hawaiʻi, Brasher et al. (2006) found that developed sites, represented by a higher percentage of pool channel units, substrate embeddedness, siltation, and shallower depths with decreased streamflow velocities, were characterized by introduced species, while undeveloped sites were characterized by native species. Common species associated with developed sites included Green Swordtail (*Xiphophorus helleri*), Bristle-nose Catfish (*Ancistrus* sp.), molly species hybrids (*Poecilia sphenops*), Red Swamp Crayfish (*Procambarus clarkii*), Tahitian Prawn (*Macrobranchium lar*), and Red Cherry Shrimp (*Neocaridina denticulata sinensis*), however Tahitian Prawn was additionally found in undeveloped sites along with native species.

In Hawaiʻi, the primary concern of introduced stream species are the potential impacts to native stream fauna (Brasher 2003). These introduced species are considered to reduce native populations directly and indirectly through predation (Lahee et al. 2004), competition for space and food resources (McRae et al. 2013), and the introduction of parasites and diseases (Font & Tate 1994). In addition, introduced species alter ecosystem dynamics, such as sediment and nutrient dynamics and trophic interactions (Yamamoto & Tagawa 2000, Holitzki et al. 2014), which could degrade the suitable stream environments for native species. It is important to understand the in-stream environmental use of introduced species to further the knowledge of their impact on Hawaiʻi's native stream fauna and ecosystems.

Information on introduced species use of in-stream environments will allow for the evaluation of impacts to native species by determining the amount of environmental overlap between species. This study will inform future studies that investigate introduced-native interactions. This information will improve the fundamental understanding of the in-stream environments of introduced species on tropical island systems, further advancing future management and conservation planning.

The primary objective of this chapter was to determine the in-stream attributes that characterize the supporting environments of select introduced species. We aimed to answer the following questions:

(1) How do in-stream environmental attributes vary among survey sites with introduced species, and which attributes exhibit the greatest variation?
(2) Do introduced species exhibit strong associations with particular in-stream environmental attributes or do introduced species occur across all variations in in-stream attributes (i.e., generalist use of environments)?
(3) What in-stream environmental attributes are favorable for biological invasions in Hawaiian streams?

This objective was addressed by conducting multivariate analyses, including principle component analysis (PCA) and canonical component analysis (CCA), and by fitting zero-inflated models using the abundance and presence-absence datasets, and their respective in-stream environmental attributes.

2.2 Methods

2.2.1 Study design

The examination of species associations with in-stream environments was conducted for two sets of data: surveyed in-stream environmental attributes from the abundance dataset and surveyed in-stream environmental attributes from the the presence-absence dataset. To conduct analyses without missing attributes, in-stream attributes in each dataset were reduced to find an agreement between the number of surveys and the number of attributes included. The number of taxa investigated were then selected based on potential ecological impacts. The resulting datasets were examined using ordination techniques and zero-inflated models.

2.2.2 In-stream environmental attribute selection

Due to the incomplete set of in-stream environmental attributes recorded in surveys from each dataset, in-stream attributes were reduced to evaluate taxon associations for surveys with a complete set of attributes. This was done by weighing the number in-stream environmental attributes versus the number of surveys with complete records, as a higher number of surveys was related the number of taxa included. This process resulted in the selection of 1315 abundance surveys that included the in-stream attributes channel unit, substrate, depth, and temperature, and 64 presence-absence surveys that included the attributes channel unit, modified status, temperature, dissolved oxygen, specific conductance, and pH. Statistical metrics (e.g., mean, maximum, minimum, and standard deviation) were summarized for quantitative variables (Table 2.1) and qualitative variables (Table 2.2).

2.2.3 Taxa selection

Taxa included this assessment were selected based on management concerns, with respect to the perceived impact to native species. Management concern was evaluated by personal communications with local stream biologist Glenn Higashi (Hawaiʻi DAR, DLNR), Dan Polhemus (U.S. Fish and Wildlife Service), and Cory Yap (Pacific Biosciences Research Center), and by literature. Groups of taxa selected included all poeciliid (*Poeciliidae*), cichlid (*Cichlidae*), centrarchid (*Centrarchidae*), salmonid (*Salmonidae*), and catfish species (Siluriformes; reviewed in Hawaii Stream Assessment 1991), as well as miscellaneous taxa, such as Tahitian Prawn (*Macrobrachium lar*; reviewed in Hawaii Stream Assessment 1991), Red Swamp Crayfish (*Procambarus clarkii*; reviewed in Brasher 2003), American Bullfrog (*Rana catesbiana*; reviewed in Snow & Witmer 2010), and Pond Loach (*Misgurnus anguillicaudatus*; reviewed in Maciolek 1984). In this assessment, the taxon tilapia was supplemented to include biological information from the tilapia fishes identified at the species level, including Blackchin Tilapia (*Sarotherodon melanotheron*), Mozambique Tilapia (*Oreochromis mossambicus*), and Red Belly Tilapia (*Tilapia zillii*). This process resulted in 15 taxa selected from the abundance dataset, and 11 taxa selected from the presence-absence dataset (Table 2.3).

2.2.4 Multivariate analysis

Ordination techniques are commonly used to describe relationships between species composition patterns and the underlying environmental gradients which influence these patterns (Jongman et. al 1995). Principal component analysis (PCA) were conducted to assess the dominate in-stream environmental attributes and their association among stream surveys with introduced species. PCA transforms a number of possibly correlated variables into a smaller number of uncorrelated principal components. The first principal component accounts for as much of the variability in the data as possible, and each succeeding component accounts for the remaining variability. The first four principle components (i.e., axes) were reported as these account for most of the overall variance explained.

Further, canonical correspondence analysis (CCA) was conducted to analyze the associations between taxa and in-stream environmental attributes. CCA is commonly used in ecological studies to summarize variation in the relative frequencies of response variables (e.g., species abundance or presence) due to explanatory variables (e.g., in-stream attributes; Lepš & Šmilauer 2003).

The assumptions of PCA and CCA included independent predictor variables and normally distributed predictor and response variables. To assess the independence of predictor variables, correlations between in-stream attributes were assessed via a Kendall rank correlation test (Hollander & Wolfe 1973) using the R Statistical Program (R Core Team 2017). The Kendall rank correlation is a non-parametric test used to estimate a rank-based measure of association between paired variables. In-stream attributes were evaluated for correlation coefficients greater than an absolute value of 0.7, however no attributes exceeded this value in either dataset. To meet the ordination assumption of normally distributed variables, all non-normally distributed in-stream attributes were transformed (see below) so that they were approximately normally distributed. Continuous in-stream attributes (e.g., temperature, depth, pH)were log transformed, and percentage variables (e.g., substrates) were converted to proportion and then arc-sine square root transformed (following Cooper et al. 2016). Taxa count data from the abundance dataset were assessed for normality and were transformed by adding a small value (i.e., 0.01) and log transformed to down-weight large numbers and account for variation in observations. Prior to analysis, the explanatory variables, i.e., in-stream attributes, were standardized so that the mean was equal to zero and standard deviation was equal to one.

All selected taxa were included in the CCAs, regardless of the frequency of survey occurrence. Traditionally it has been a common practice to exclude species that occurred in less than five percent of surveys. However, Lepš and Hadincová (1992) showed that excluding species that occurred in less than five percent of the surveys did not significantly influence the results, as the results are primarily dependent upon the dominant species. Additionally, due to the inherent nature of the data, including sparsely-distributed species, the removal of rare taxa would have resulted in the loss of many taxa from the analysis. Table 2.3 identified taxa in each dataset that occurred in less than five percent of surveys.

Principal component analysis and CCA ordination techniques were conducted on each dataset using the statistical program CANOCO 5 (Microcomputer Power, Ithaca, NY, USA; Ter Braak & Šmilauer 2012). For both PCA and CCA, analysis-specific results were reported for the first four axes. PCA analyses were interpreted by evaluating the variation explained by axes, and the corresponding response score of environmental variables. Response scores represented regression coefficients, which indicate the magnitude (from 0 to 1) and direction (+/-) of a variables importance to a given axis. CCA analyses were interpreted by evaluating the amount of variation in taxa composition explained by dominant explanatory variables, i.e., in-stream environmental attributes. The relative effect of each explanatory variable was evaluated per axis using the response score to indicate direction and variation, and t-value to evaluate the size of effect. The absolute value of the t-value indicated the magnitude of the effect, and t-values less than 2.1 in absolute value indicated that the variable did not contribute significantly to the fit of response data relative to the contributions of the other explanatory variables in the analysis (Ter Braak & Šmilauer 2012). Ordination biplots were inspected to evaluate the associations (i.e., correlations) between taxa and in-stream environmental attributes.

2.2.5 Zero-inflated models

Based on framework of generalized linear models, zero-inflated models are utilized to quantify relationships between species and environmental characteristics when species abundance or occurrence data has a large number of zeros (Potts & Elith 2006). Datasets are considered zero-inflated when the number of zeros is large enough that the data do not fit standard distributions such as normal, Poisson, binomial, or negative-binomial distributions (Martin et al. 2005). Zero inflation is problematic to an analysis if zeros result from processes not directly investigated, which obscures the results. Second, zero inflation is a source of over dispersion, which describes the presence of greater variability in a dataset than would be expected by models, resulting in artificially small confidence intervals and *p* values. Zero-inflated models exhibit advantages as compared to generalized linear model by simultaneously addressing and remedy auxiliary reasons that species are absent from sites.

Zero-inflated count or occurrence data can occur due to true negative or false negative observations (Potts & Elith 2006). True negative observations are zeros that occurred due to unsuitable conditions. False negative observations are zeros that occurred for reasons such as patchy species distributions, experimental design, and observer error (i.e., species is present but not detected). Zero-inflated models aim to differentiate between true negative and false negative observations by modeling each type of observation (e.g., true negative and false negative) with a specified distribution and predictors. Therefore, these models are advantageous for characterizing the in-stream environmental attributes of introduced stream species, due to the suspected high occurrence of false negative observations that arise when species have not been introduced to a given stream system. Essentially, these models allow for the differentiation of zeros as either unsuitable environmental conditions or a lack of introduction, and thus improve the model results for species associations with in-stream environmental attributes.

Zero-inflated negative binomial models were fit for taxa in the abundance and presence-absence datasets that had at least 10 unique survey occurrences (see Table 2.3 for the number of survey occurrences per taxon) using the pscl package (Zeileis et al. 2008; Jackman 2017). For both datasets, zero occurrences (i.e., false negatives) were predicted using distance to the nearest road and site elevation. This was conducted in order to quantify the chance of lack of introductions, as roads serve as access points and as most human actions and development occur at low elevations (Brasher et al. 2006). Both variables were log transformed. Information for roads were obtained from the Hawaiʻi Statewide Planning and Geographic Information System Program (http://planning.hawaii.gov/gis/), and information for elevation were obtained from island specific digital elevation models from the University of Hawaiʻi at Manoā Costal Geology Group (http://www.soest.hawaii.edu/coasts/data/). To simplify the in-stream attributes used for the abundance dataset, the substrate classes "sediment" and "sand" were combined as fine substrates, and the classes "cobble" and "boulder" were combined as large substrates. For each dataset, individual zero-inflated negative binomial models were initially fit for selected taxa using all in-stream attributes selected for the respective dataset. Non-significant predictors (p value > 0.10) were removed in a stepwise fashion to find the best fit model, using the Akaike Information Criterion (AIC) to evaluate each removal (Symonds & Moussalli 2011). AIC is an estimator of the relative quality of statistical models for a given set of data by evaluating goodness of fit and the number of predictors included, and thus provided a means for model selection. This process was repeated until AIC was minimized or until all attributes included in the model exhibited p values < 0.10.

2.3 Results

2.3.1 Principal component analyses

The PCA of in-stream environmental attributes in the abundance dataset (1315 surveys; Table 2.4, Figure 2.1) explained 42.7% of the variation, and indicated that the channel units pool and run contributed the most to the primary axis, while boulder and sediment contributed the most to the secondary axis (See Table 2.4 for a summary of the first four axes). The PCA of in-stream attributes in the presence-absence dataset (74 surveys; Table 2.5, Figure 2.2) explained 77.1% of the variation, and indicated that channel units pool and run, and modified status contributed the most to the primary axis. While modified status and DO contributed the most to the secondary axis (See Table 2.5 for a summary of the first four axes). Overall, the PCAs indicated that the in-stream environmental attributes that explained the most variation among stream survey sites were channel units (pool and run), substrate type (sediment and boulder), and DO.

2.3.2 Canonical correspondence analyses

The CCA analysis conducted on the abundance dataset (15 taxa, 1315 surveys) resulted in in-stream environmental attributes explaining 4.4% of the total variation in taxa composition (see Table 2.6 for a summary of the first four axes, and Figure 2.3 for the corresponding taxa plot). Taxa variation was primarily driven by water temperature, and secondarily driven by depth and the substrates sand and sediment. The low values of explained variation were likely due to the large number of surveys relative to low frequencies of taxa occurrence. The taxa plot indicated that the majority of the taxa occurred near the center of the plot associated with pool and run channel units, or in the direction of smaller substrates.

A few taxa, including American Bullfrog and tilapia occurred as outliers in the direction of increasing temperature.

The CCA analysis conducted on the presence-absence dataset (10 taxa, 64 surveys) showed that in-stream environmental attributes explained 23.0% of the total variation in taxa composition (see Table 2.7 for a summary of the first four axes, and Figure 2.4 for the corresponding taxa plot). Taxa variation was primarily driven by temperature and specific conductance, and secondarily driven by DO. The taxa plot indicated that the majority of the taxa occurred near the center of the plot associated with pool and run channel units, along a gradient of temperature and DO. While tilapia and Common Molly were associated with increased temperature and specific conductance.

2.3.3 Zero-inflated models

Models were successfully fit to all taxa in the abundance dataset with 10 or more unique survey occurrences (7 taxa, Table 2.8). Of the in-stream attributes assessed, temperature, depth, large substrates, and fine substrates were the most important predictors for the taxa. Distance to roads or elevation were found to be significant predictors of zero occurrences for all taxa except on Green Swordtail. For the taxa which false absence (i.e., lack of introduction sources) were accounted for, taxa were generally absent from sites further from roads or at higher elevation. However, the Tahitian Prawn exhibited the opposite trends – the taxon was absent from sites closer to roads ($p \leq 0.001$) and at lower elevations ($p \leq 0.001$).

Models were fit to all taxa in the presence-absence dataset with 10 or more unique survey occurrences (5 taxa, Table 2.9). However, this assessment failed to identify significant predictors for taxa, except DO for Guppy occurrence. The lack of significant results was likely due the small number of surveys (i.e., 64 surveys) relative to the number of predictors (i.e., six attributes) investigated.

The assessment of the abundance dataset indicated that depth, temperature (temp), and substrate classes exhibited the most significant effects on the taxa investigated. Additionally, the abundance dataset assessment suggested the prominent significance of zero inflation predictors (e.g., distance to roads and elevation) among taxa. The identification of significant sources of zero inflation in these models improved the accuracy of the likelihood tests conducted with in-stream attributes, and therefore resulted in more accurate assessments of taxon associations with in-stream environmental attributes.

2.4 Discussion

This study examined introduced stream species use of in-stream enviornmental attributes throughout the five main Hawaiian Islands by evaluating the variation among in-stream attributes as well as taxon associations with in-stream attributes. This assessment indicated that substrate type, followed by channel unit, were the primary sources of variation for in-stream environmental attributes. While, the in-stream attributes depth, temperature, and substrate type had the largest influence on introduced stream species. The use of in-stream attributes by introduced species varied among the taxa investigated, and indicated that some species (e.g. Common Molly and Western Mosquitofish) exhibited generalist use of in-stream attributes (i.e., utilizing warm, shallow, pool habitats with fine substrates) while others (e.g., Tahitian Prawn and Guppy) exhibited use of in-stream environments more characteristic of pristine streams(e.g., cooler, deeper waters with larger substrates).

The analyses conducted with the abundance dataset were considered to be a more accurate representation of variation among in-stream attributes and taxon associations with in-stream attributes, given number of surveys and the spatial scale at which the surveys were conducted. However, the presence-absence dataset included certain in-stream attributes (e.g., dissolved oxygen, specific conductance, pH, and modified status) and taxa (e.g., Bristle-nosed Catfish) that were not available in the abundance dataset assessment.

The PCA indicated that the primary differences among stream survey sites were channel units (pool and run), and substrate types (sediment and boulder). This assessment showed prominent correlations among various channel units and other in-stream attributes, including run channel units with cobble substrates, riffle channel units with boulder substrates, side pool channel units with sediment, sand, detritus, and increased temperature, and plunge pool channel units with increased depth. Some channel units exhibited greater variation in in-stream attributes, e.g., plunge pool channel units where characterized by either boulder or bedrock, while pool channel unints were characterized by either bedrock or fine substrates and detritus. These relationships support other studies (e.g., Frissell et al. 1986, Brasher et al. 2006, Higashi & Nishimoto 2007). These prominent correlations among channel units and other in-stream attributes (e.g., depth, temperature, and substrate) suggested that stream environments have distinct patterns, which support the introduced stream fauna in Hawaiʻi. While not directly investigated here, these patters most likely reflect elevation and the related erosional processes to some degree. This process details more erosion occurring at higher elevations where stream slopes are steeper, and the deposition of these substrates at lower elevations where stream slopes are gentler, resulting in larger substrates in higher elevations and finer substrates at lower elevations (Frissell et al. 1986).

The CCA indicated that water temperature was the dominant in-stream environmental attribute that explained the variation in taxa composition. Water temperature had the largest influence on tilapia and American bullfrog. Tilapia was associated with the highest temperatures (mean = 26.4 °C, max. = 29.2 °C), followed American Bullfrog (mean = 24.1 °C, max. = 29.1 °C), while tilapia occurred in shallower sites with finer substrates and American Bullfrog occurred in deeper sites with larger substrates. Of the various tilapia species which occur in Hawaiʻi (according to Yamamoto & Tagawa 2000) the upper temperature limits for many species range from 35 °C to approximately 40 °C (Mozambique Tilapia: Philippart & Ruwet 1982, Stauffer 1986; Redbelly Tilapia and Longfin Tilapia: Froese & Pauly 2017). The upper temperature limit for the American Bullfrog is approximately 37 °C (Lillywhite 1970, Govindarajulu et al. 2006). For reference, the mean and maximum water temperatures recorded in the abundance dataset were 21.5 °C and 31.5 °C, respectively, all under the maximum temperature tolerances documented in previous studies. However, no surveys in this study were conducted in highly-urbanized areas (e.g., Honolulu area) which likely exhibit the warmest water temperatures. Therefore, the maximum temperature recorded for taxa in this study might not represent the upper limit for the taxon's habitat use in Hawaiʻi. Overall this indicated a preference for warmer temperatures for these taxa and suggests high temperatures do not limit the in-stream environmental use of these taxa for Hawaiian streams outside of highly-urbanized areas. Differences among these temperature tolerant taxa (e.g., American Bullfrog and tilapia) were influenced by varying preferences for depth, substrate, and possibly salinity.

The CCA indicated that Green Swordtail, Guppy, Western Mosquitofish, Banded Jewelfish, Pond Loach, and Tahitian Prawn all occurred near the origin of the CCA plot along with the channel units: run, pool, and side pool, which suggests in-stream enviornmental use typical of these generalist species.

However, no species were strongly associated with the channel units riffle, cascade, or plunge pool, which are typically characterized by turbulent fast flowing water. This indicated that introduced species investigated here do not commonly utilize these channel units. These results agree with other studies conducted in Hawaiʻi which indicated that introduced poeciliid fishes (e.g., Guppy, Western Mosquitofish, Green Swordtail, etc.) typically utilized pool (Brasher et al. 2006) or run (McRae et al. 2013) channel units compared to riffle channel units.

While Common Molly, Cuban Limia, Convict Cichlid, Armored Catfish, and Blackchin Tilapia all occurred in sites with sand, gravel, or cobble substrates. Of these taxa, Blackchin Tilapia, Armored Catfish, and the closely related Bristle-nosed Catfish (included in presence-absence CCA) are of particular concern to natural resource managers due to their wide environmental tolerances, high population densities, and their potential to compete with native stream species for food and space resources in streams (Yamamoto & Tagawa 2000). Blackchin Tilapia has been reported as prominent fish in the estuarine areas on Oʻahu (Englund et al. 2000) and Kauaʻi (Brown et al. 1999). Our study added to this by showing that these fish are moving upstream into complete freshwater environments (surveys from the abundance dataset was all conducted in complete freshwater sites) where they are likely to overlap with native stream species. Armored Catfish and the related Bristle-nosed Catfish have been the most recently introduced fishes to become prominent in certain areas in Hawaiʻi. Both species are commonly found in urbanized streams also in addition to also occurring in natural streams (Cory Yap, Pacific Biosciences Research Center, personal communication; Brasher et al. 2006), which represents the fishes ability to tolerate a range of environmental conditions. In the presence-absence CCA of study Bristle-nosed Catfish was associated with all pool channel units (e.g., pool, plunge pool, side pool) with relatively low DO (mean DO for Bristle-nosed Catfish from presence-absence dataset = 1.73 mg/L).

In-stream environmental associations assessed using zero-inflated models indicated that depth, temperature, and substrate type were the most important predictors for taxa investigated (e.g., Western Mosquitofish, Green Swordtail, Guppy, Common Molly, Tahitian Prawn, Red Swamp Crayfish, and American Bullfrog). This agreeed with the CCA findings; furthermore, by accounting for zero inflation, taxon-specific assessments using zero-inflated models represented more accurate taxon associations with in-stream attributes compared to the CCA. All poeciliid taxa assessed via zero-inflated models (e.g., Green Swordtail, Guppy, Common Molly, and Western Mosquitofish) were associated with fine and medium substrates, which corresponds to the typical in-stream environmental use of these taxa. Western Mosquitofish was associated with increased water temperatures which is typically expected of poeciliid fishes (Hernández & Bückle 2002, Froese & Pauly 2017); however, Green Swordtail and Guppy were associated with decreased temperatures, which indicated a preference for cooler water sites. Green Swordtail exhibited a negative response to detritus substrates, which are commonly associated with low DO and low streamflow velocity environments, this indicated a possible preference for less disturbed environments with higher DO and streamflow velocities. Additionally, Guppy was associated with bedrock substrates which are possibly indicative of mid-to-higher elevation streams that occasionally experience high velocity flow events (Seidl et al. 1994).

Of the non-fish taxa assessed with zero-inflated models, the Tahitian Prawn and Red Swamp Crayfish were associated with deeper waters and large substrates, likely reflecting their benthic use of stream environments and preference for sheltered areas (e.g. crevices and burrows; Yamamoto & Tagawa 2000). Additionally, Tahitian Prawn was associated with bedrock substrates. As previously noted this may possibly indicative of mid-to-higher elevation stream bed substrates that occasionally experience high velocity streamflow events (Seidl et al. 1994). American Bullfrog exhibited a positive association with detritus substrates and increased temperature, which indicated a preference for warm, low velocity streamflow environments. This was expected as amphibians require warm environments to self-regulate their body temperature. Additionally, the presence of still waters and the associated dense emergent vegetation has been suggested to be an important in-stream environmental characteristic for this species (Bury & Whelan 1984).

2.5 Conclusion

This assessment indicated that temperature, depth, and substrate type had the largest impact on the use in-stream environments for introduced stream species. This investigation found that some taxa adhered to the general ideology that introduced stream species typically utilize warm, shallow, low velocity pools with fine substrates, specifically Common Molly and Western Mosquitofish. The amount of advantageous in-stream environments for these taxa are expected to expand with increasing anthropogenic disturbances and future climate change. However, many taxa such as Tahitian Prawn, American Bullfrog, Red Swamp Crayfish, Green Swordtail, Guppy, Smallmouth Bass, and potentially the Bristle-nosed Catfish, deviate from this paradigm by utilizing different combinations of cooler, deeper waters, with larger substrates in Hawaiʻi. Additionally, evidence suggests that Tahitian Prawn, and to a lesser extent, Guppy occur in stream environments that frequently experience high velocity stream flows, this characteristics has been previously suggested to limit the occurrence of introduced stream species in Hawaiʻi. Furthermore, the use of in-stream environments of introduced species may differ from their native range due to biotic interactions with other species (e.g., lack of predators or competition with other introduced species). The use of stream environments by by introduced species described herein served to complement the corresponding assessment of species associations with landscape variables (Chapter Three), to provide a multi-scale assessment of introduced species in Hawaiʻi.

Chapter Two Tables

Table 2.1. Descriptive statistics including mean, minimum (min), maximum (max), and standard deviation (sd) of quantitative in-stream environmental attributes in the abundance (1315 total surveys) and presence-absence (64 total surveys) datasets. Substrate type (Substrate) indicates the percent cover of the classes: detritus, sediment, sand, gravel, cobble, boulder, and bedrock.

Attribute	Statistic	Dataset	
		Abundance	Presence-absence
Substrate: Detritus (%)	mean	2.71	-
	min-max	0-100	-
	sd	9.55	-
Substrate: Sediment (%)	mean	3.41	-
	min-max	0-100	-
	sd	12.87	-
Substrate: Sand (%)	mean	6.40	-
	min-max	0-100	-
	sd	15.18	-
Substrate: Gravel (%)	mean	18.75	-
	min-max	0-100	-
	sd	21.01	-
Substrate: Cobble (%)	mean	25.61	-
	min-max	0-100	-
	sd	24.43	-
Substrate: Boulder (%)	mean	34.59	-
	min-max	0-100	-
	sd	30.60	-
Substrate: Bedrock (%)	mean	8.52	-
	min-max	0-100	-
	sd	24.71	-
Depth (m)	mean	0.43	-
	min-max	0.03-2.44	-
	sd	0.27	-
Temperature (C)	mean	21.54	23.84
	min-max	13.00-30.31	19.22-32.02
	sd	2.11	2.05
Specific Conductance (mS)	mean	-	3.71
	min-max	-	0.05-47.60
	sd	-	11.37
Dissolved Oxygen (mg/L)	mean	-	5.96
	min-max	-	0.27-9.91
	sd	-	2.35
pH	mean	-	7.28
	min-max	-	5.84-8.11
	sd	-	0.49

Table 2.2. Summary of the qualitative in-stream environmental attributes in the abundance (1315 total surveys) and presence-absence (64 total surveys) datasets, including the number of surveys per attribute category.

Attribute	**Categories**	**Dataset**	
		Abundance	**Presence-absence**
Channel Unit	run	619	31
	riffle	129	3
	pool	329	27
	plunge pool	66	3
	side pool	159	0
	cascade	13	0
Modified Status	natural	-	54
	modified	-	10

Table 2.3. Selected taxa from the abundance and presence-absence datasets for the analysis of in-stream environmental attributes, with the number of survey occurrences for each dataset. (*) indicated taxa with occurrences in less than 5% of samples per dataset. Code indicates the two-letter taxon identifier used for analyses.

Scientific Name	Common Name	Code	Survey Occurrences per Dataset	
			Abundance	Presence-absence
Ancistrus cf. temminckii	Bristle-nosed Catfish	BC	-	3*
Archocentrus nigrofasciatus	Convict Cichlid	CC	4*	2*
Gambusia affinis	Western Mosquitofish	WM	33*	26
Hemichromis fasciatus	Banded Jewelfish	BJ	4*	-
Hypostomus watwata	Armored Catfish	AC	5*	-
Limia vittata	Cuban Limia	CL	1*	-
Macrobrachium lar	Tahitian Prawn	TP	752	7
Micropterus dolomieu	Smallmouth Bass	SB	4*	2*
Misgurnus anguillicaudatus	Pond Loach	PL	8*	-
Poecilia reticulata	Guppy	GU	124	14
Poecilia sphenops	Common Molly	CM	41*	2*
Procambarus clarkii	Red Swamp Crayfish	RS	36*	12
Rana catesbiana	American Bullfrog	AB	13*	7
Sarotherodon melanotheron	Blackchin Tilapia	BT	2*	-
Tilapiini (*Cichlidae*) spp.	Tilapia	TI	9*	17
Xiphophorus helleri	Green Swordtail	GS	270	21

Table 2.4. Principal component analysis results of the in-stream environmental attributes from the abundance dataset (1315 surveys). Eigenvalues, cumulative explained variation, and explanatory variable responses were reported for the first four PCA axes. In-stream attributes detritus, sediment, sand, gravel, cobble, boulder, and bedrock describe substrate type. The in-stream attributes side pool (s.pool), run, riffle, plunge pool (p.pool), cascade, and pool describe channel unit. The attribute temperature is abbreviated as temp.

Summary:				
Statistic	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.1345	0.1075	0.0944	0.0909
Explained variation (cumulative)	13.45	24.20	33.64	42.73

Explanatory Variables:				
Attributes	**Resp.1**	**Resp.2**	**Resp.3**	**Resp.4**
detritus	0.2079	0.3214	0.2123	0.2616
sediment	0.1622	0.5435	-0.0587	0.1348
sand	-0.0696	0.4005	-0.1366	0.1723
gravel	-0.3832	0.2567	-0.1214	-0.4772
cobble	-0.5079	-0.1036	0.0467	-0.5377
boulder	0.0083	-0.6257	0.4327	0.4176
bedrock	0.5688	-0.0374	-0.3866	0.0859
depth	0.4895	-0.3408	-0.2004	-0.1534
temp	-0.039	0.3573	0.1109	0.3745
run	-0.6548	-0.1315	-0.5795	0.3993
p.pool	0.3900	-0.3154	-0.2178	0.0272
cascade	-0.0518	-0.0595	0.0977	-0.1833
pool	0.6227	0.2715	0.003	-0.3859
riffle	-0.0220	-0.2445	0.4493	-0.1793
s.pool	-0.0503	0.2930	0.5895	0.1022

Table 2. 5. Principal component analysis results of the in-stream environmental attributes from the presence-absence dataset (64 surveys). Eigenvalues, cumulative explained variation, and explanatory variable responses were reported for the first four PCA axes. The in-stream attributes run, riffle, plunge pool (p.pool), and pool describe channel unit. The attributes modified and natural describe modified status. The variables dissolved oxygen, specific conductance, and temperature are abbreviated as DO, SC, and temp, respectively.

Summary: **Statistic**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.2516	0.2178	0.1677	0.1335
Explained variation (cumulative)	25.16	46.94	63.71	77.06

Explanatory Variables: **Attributes**	**Resp.1**	**Resp.2**	**Resp.3**	**Resp.4**
temp	-0.1398	-0.4879	0.5800	0.2390
DO	-0.4948	0.6283	0.1171	-0.0934
pH	-0.3785	-0.0559	0.4497	-0.612
SC	0.4721	-0.284	0.6244	0.027
riffle	0.1106	0.2850	-0.247	0.7381
run	-0.7522	0.1544	0.4391	0.1842
p.pool	-0.0288	0.5086	-0.3712	-0.4752
pool	0.7262	-0.4958	-0.1797	-0.299
modified	0.6243	0.6526	0.3940	0.0026
natural	-0.6243	-0.6526	-0.3940	-0.0026

Table 2.6. Canonical correspondence analysis results of taxa composition with in-stream environmental attributes from the abundance dataset (1315 surveys, 15 taxa, 14 degrees of freedom). Eigenvalues, cumulative explained variation, and explanatory variable responses (regression coefficients and T values, abbreviated as Regr and TVal, respectively) were reported for the first four CCA axes. In-stream attributes detritus, sediment, sand, gravel, cobble, boulder, and bedrock described substrate type. The in-stream attribute side pool (s.pool), run, riffle, plunge pool (p.pool), cascade, and pool described channel unit. The attribute temperature was abbreviated as temp.

Summary:

Statistic	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.1673	0.1362	0.0472	0.031
Explained variation (cumulative)	1.640	2.980	3.450	3.750
Pseudo-canonical correlation	0.4687	0.3956	0.241	0.2137
Explained fitted variation (cumulative)	37.00	67.11	77.55	84.41

Explanatory Variables:

Attributes	**RegrE.1**	**RegrE.2**	**RegrE.3**	**RegrE.4**	**TValE.1**	**TValE.2**	**TValE.3**	**TValE.4**
detritus	-0.0236	-0.1228	-0.1275	-0.0669	-0.3310	-1.3961	-0.8357	-0.3862
sediment	0.1902	0.5234	0.2163	-0.9101	2.1357	4.7694	1.1363	-4.2131
sand	-0.0028	0.4691	-0.1519	-0.0472	-0.0315	4.2342	-0.7903	-0.2164
gravel	-0.2975	0.2239	-0.2352	-0.8516	-2.8976	1.7695	-1.0716	-3.4198
cobble	-0.3140	0.1959	0.0716	-0.4271	-2.6972	1.3661	0.2879	-1.5130
boulder	-0.1655	-0.0644	0.1120	-1.2376	-1.1560	-0.3648	0.3660	-3.5636
bedrock	0.0755	0.0070	0.2746	-1.0193	0.5536	0.0414	0.9420	-3.0816
depth	-0.2763	-0.3920	0.0523	0.2554	-4.3941	-5.0597	0.3890	1.6742
temp	0.6911	-0.3069	-0.3200	0.1005	11.8212	-4.2599	-2.5611	0.7087
run	-0.2935	0.2794	-0.6174	-0.2709	-3.1568	2.4387	-3.1072	-1.2012
plunge pool	-0.1319	-0.0998	-0.3797	-0.0848	-1.8907	-1.1609	-2.5468	-0.5011
cascade	-0.0566	-0.1197	-0.1947	-0.1191	-0.9645	-1.6555	-1.5523	-0.8368
pool	-0.1697	0.2184	0.1553	-0.1223	-1.8136	1.8946	0.7769	-0.5390
riffle	-0.1669	-0.1024	-0.4460	-0.4125	-2.3076	-1.1487	-2.8859	-2.3521
side pool	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Permutation Test:

Statistic	**All Axes**
pseudo-F	3.7
p value	0.002

Table 2.7. Canonical correspondence analysis results of taxa composition with in-stream environmental attributes from the presence-absence dataset (64 surveys, 10 taxa). Eigenvalues, cumulative explained variation, and explanatory variable responses (regression coefficients and T values, abbreviated as Regr and TVal, respectively) were reported for the first four CCA axes. The in-stream attributes run, riffle, plunge pool (p.pool), and pool described habitat type. The attributes modified and natural describe modified status. The attributes dissolved oxygen, specific conductance, and temperature were abbreviated as DO, SC, and temp, respectively.

Summary:

Statistic	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.4031	0.2268	0.1296	0.0939
Explained variation (cumulative)	9.660	15.10	18.20	20.45
Pseudo-canonical correlation	0.7632	0.6658	0.5952	0.5244
Explained fitted variation (cumulative)	41.96	65.57	79.05	88.82

Explanatory Variables:

Attributes	**RegrE.1**	**RegrE.2**	**RegrE.3**	**RegrE.4**	**TValE.1**	**TValE.2**	**TValE.3**	**TValE.4**
temp	0.3992	-0.5692	-0.3877	-0.0275	2.6907	-2.8973	-1.6384	-0.0967
DO	-0.0326	-0.4515	0.2917	0.3143	-0.2092	-2.1909	1.1752	1.0530
pH	0.2093	0.1918	-0.6024	-0.1138	1.4989	1.0373	-2.7048	-0.4249
SC	0.6843	0.5438	0.6341	0.1569	5.0075	3.0057	2.9094	0.5987
pool	-0.5859	-0.9068	0.7117	-3.0277	-0.8753	-1.0232	0.6666	-2.3585
run	-0.3364	-1.1764	1.0641	-2.8318	-0.5077	-1.3411	1.0070	-2.2286
riffle	-0.1715	-0.3621	0.6456	-1.3577	-0.7423	-1.1836	1.7519	-3.0636
plunge pool	-0.0865	-0.0205	0.0614	0.0108	-0.5355	-0.0959	0.2385	0.0350
side pool	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Permutation Tests:

Statistic	**All Axes**
Pseudo - F	2.1
p value	0.008

Table 2.8. Zero-inflated negative binomial model results, indicating significant in-stream environmental attributes for taxa in the abundance dataset, as well as significant predictors of zero-inflation (i.e., road and elevation). The attribute fine substrate represented a combination of sediment and sand substrate classes, the attribute medium substrate represented gravel substrate, and the attribute large substrate represented a combination of cobble and boulder substrate classes. The predictor of extra zeros, roads, was the distance to the nearest road. Variable significance was evaluated by maximum likelihood, significance codes: (***): $p \leq 0.001$, (**): $p \leq 0.01$, and (*): $p \leq 0.05$. The (+/-) following the significance code indicated the direction of the effect. Code indicated the two-letter taxon identifier used for analyses.

Scientific Name	**Common Name**	**Code**	**Detritus**	**Fine Sub.**	**Med Sub.**	**Large Sub.**	**Bedrock**	**Pool**	**Side Pool**	**Depth**	**Temp**	**Road**	**Elevation**
Gambusia affinis	Western Mosquitofish	WM		* (+)						** (+)	** (+)	** (+)	
Macrobrachium lar	Tahitian Prawn	TP			** (+)	*** (+)	*** (+)			*** (+)		*** (-)	*** (+)
Poecilia reticulata	Guppy	GU		* (+)			* (+)					*** (+)	*** (-)
Poecilia sphenops	Common Molly	CM			** (+)							* (+)	* (+)
Procambarus clarkii	Red Swamp Crayfish	RS		* (+)	*** (+)	*** (+)				*** (+)			*** (-)
Rana catesbiana	American Bullfrog	AB	*** (+)	* (+)		* (+)	* (+)				*** (+)		*** (-)
Xiphophorus helleri	Green Swordtail	GS	* (-)					* (+)	* (+)	* (+)	*** (-)		

Table 2.9. Zero-inflated negative binomial model results, indicating significant in-stream environmental attributes for taxa occurrence in the presence-absence dataset, as well as significant predictors of zero-inflation (i.e., road and elevation). The attribute dissolved oxygen was abbreviated as DO. Variable significance was evaluated by maximum likelihood, significance codes: (***): $p < 0.001$, (**): $p < 0.01$, and (*): $p < 0.05$. The (+/-) following the significance code indicated the direction effect. Code indicated the two-letter taxon identifier used for analyses.

<table>
<tr><th>Scientific Name</th><th>Common Name</th><th>Code</th><th>DO</th><th>Elevation</th></tr>
<tr><td>Gambusia affinis</td><td>Western Mosquitofish</td><td>WM</td><td rowspan="5">** (-)</td><td rowspan="5"></td></tr>
<tr><td>Poecilia reticulata</td><td>Guppy</td><td>GU</td></tr>
<tr><td>Procambarus clarkii</td><td>Red Swamp Crayfish</td><td>RS</td></tr>
<tr><td>Tilapiini (Cichlidae) spp.</td><td>Tilapia</td><td>TI</td></tr>
<tr><td>Xiphophorus helleri</td><td>Green Swordtail</td><td>GS</td></tr>
</table>

Chapter Two Figures

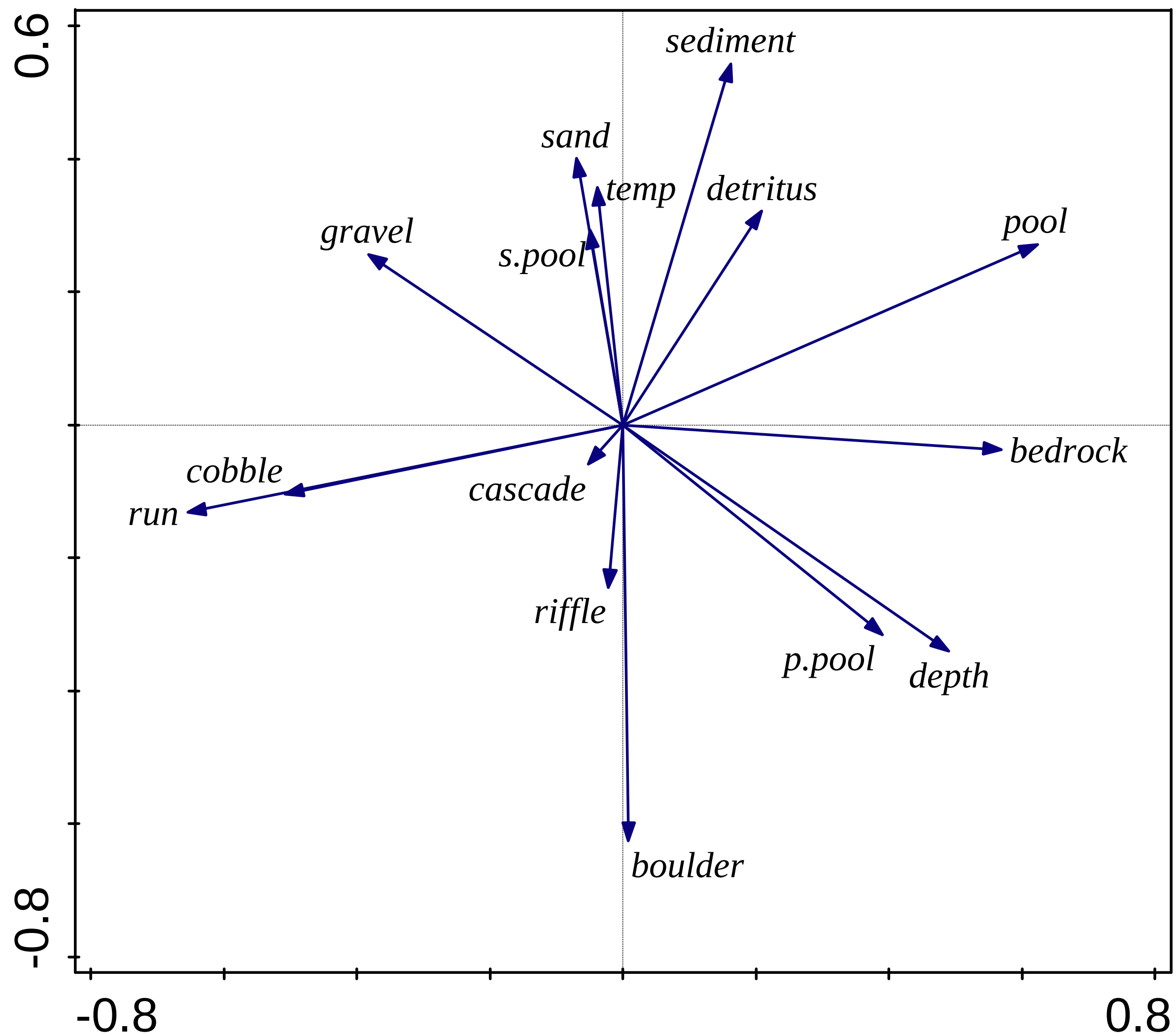


Figure 2.1. Principal component analysis biplot of the in-stream environmental attributes from the abundance data subset (1315 surveys). In-stream attributes detritus, sediment, sand, gravel, cobble, boulder, and bedrock described substrate type. The in-stream attributes side pool (s.pool), run, riffle, plunge pool (p.pool), cascade, and pool described channel unit. The attribute temperature was abbreviated as temp.

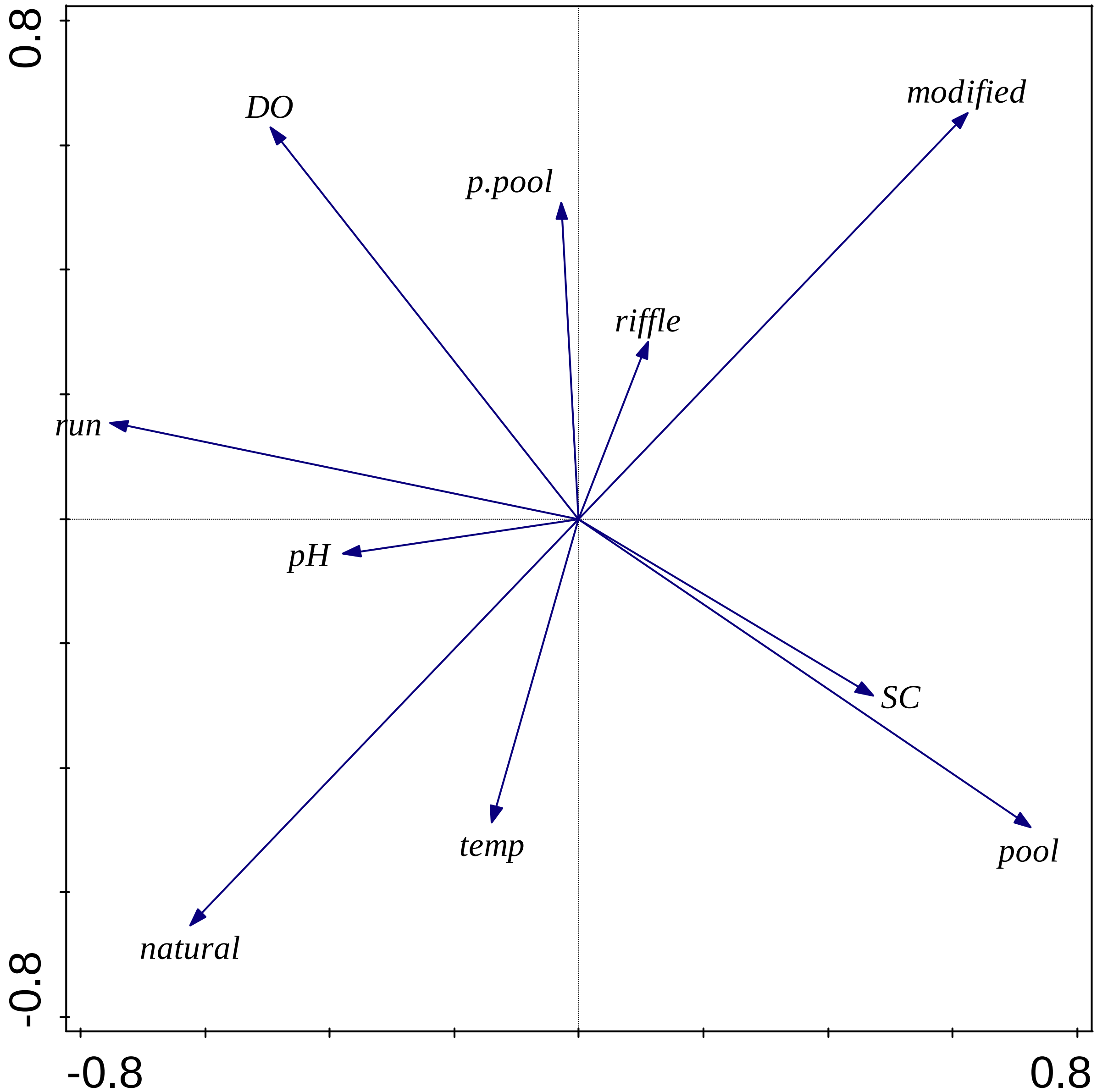


Figure 2.2. Principal component analysis biplot of the in-stream environmental attributes from the presence-absence data subset (64 surveys). The in-stream attributes run, riffle, plunge pool (p.pool), and pool described channel unit. The attributes modified and natural described modified status. The attributes dissolved oxygen, specific conductance, and temperature were abbreviated as DO, SC, and temp, respectively.

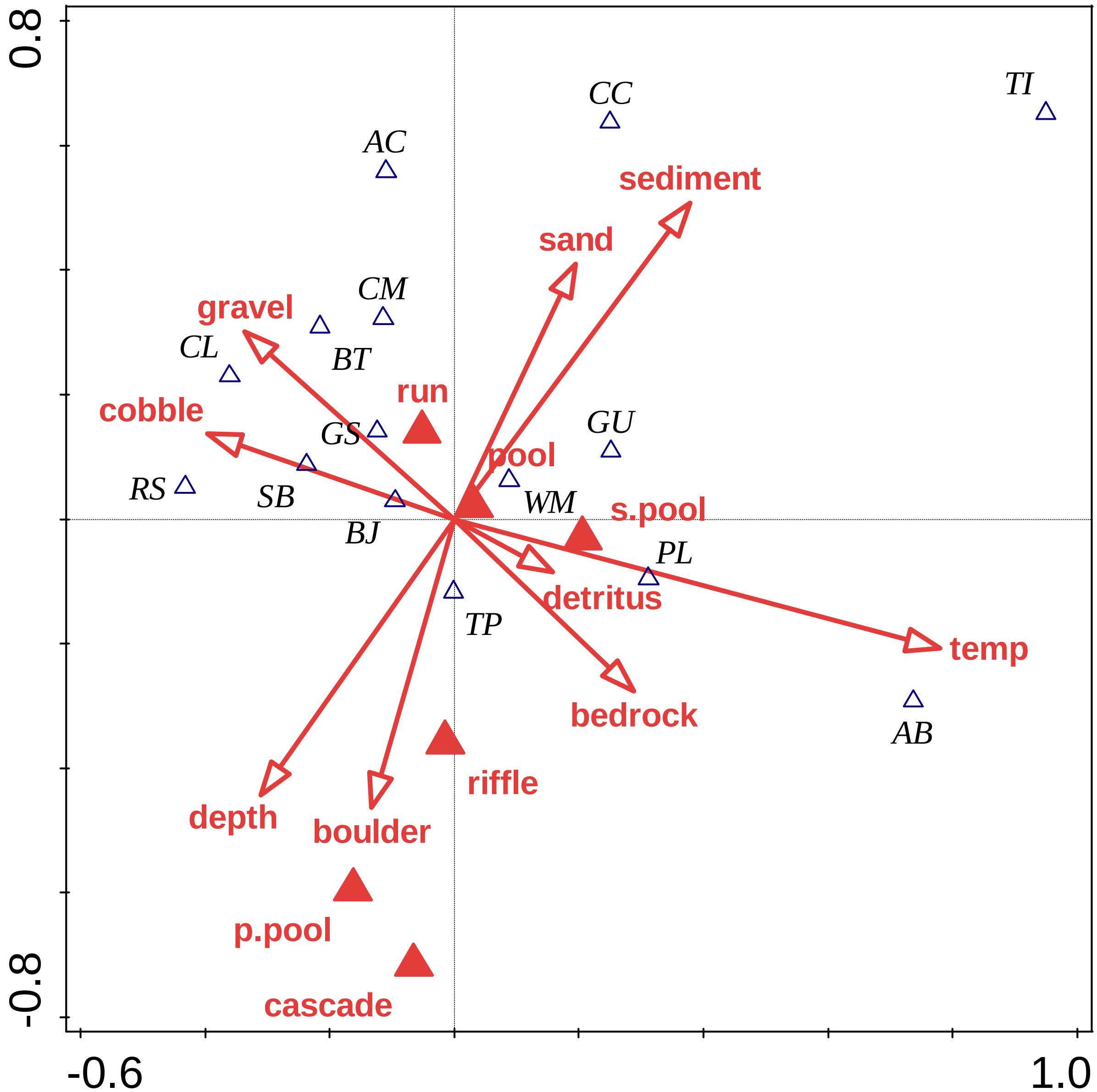


Figure 2.3. Canonical correspondence analysis biplot of taxa composition with in-stream environmental attributes from the abundance data subset (1315 surveys, 15 taxa, 14 degrees of freedom). In-stream attributes detritus, sediment, sand, gravel, cobble, boulder, and bedrock described substrate type. The in-stream attributes side pool (s.pool), run, riffle, plunge pool (p.pool), cascade, and pool described channel unit. The attribute temperature was abbreviated as temp. Taxa codes: GS = Green Swordtail, CM = Common Molly, CL = Cuban Lima, GU = Guppy, WM = Western Mosquitofish, CC = Convict Cichlid, BJ = Banded Jewelfish, BT = Blackchin Tilapia, TI = tilapia, AC = Armored Catfish, SB = Smallmouth Bass, PL = Pond Loach, TP = Tahitian Prawn, RS = Red Swamp Crayfish, AB = American Bullfrog.

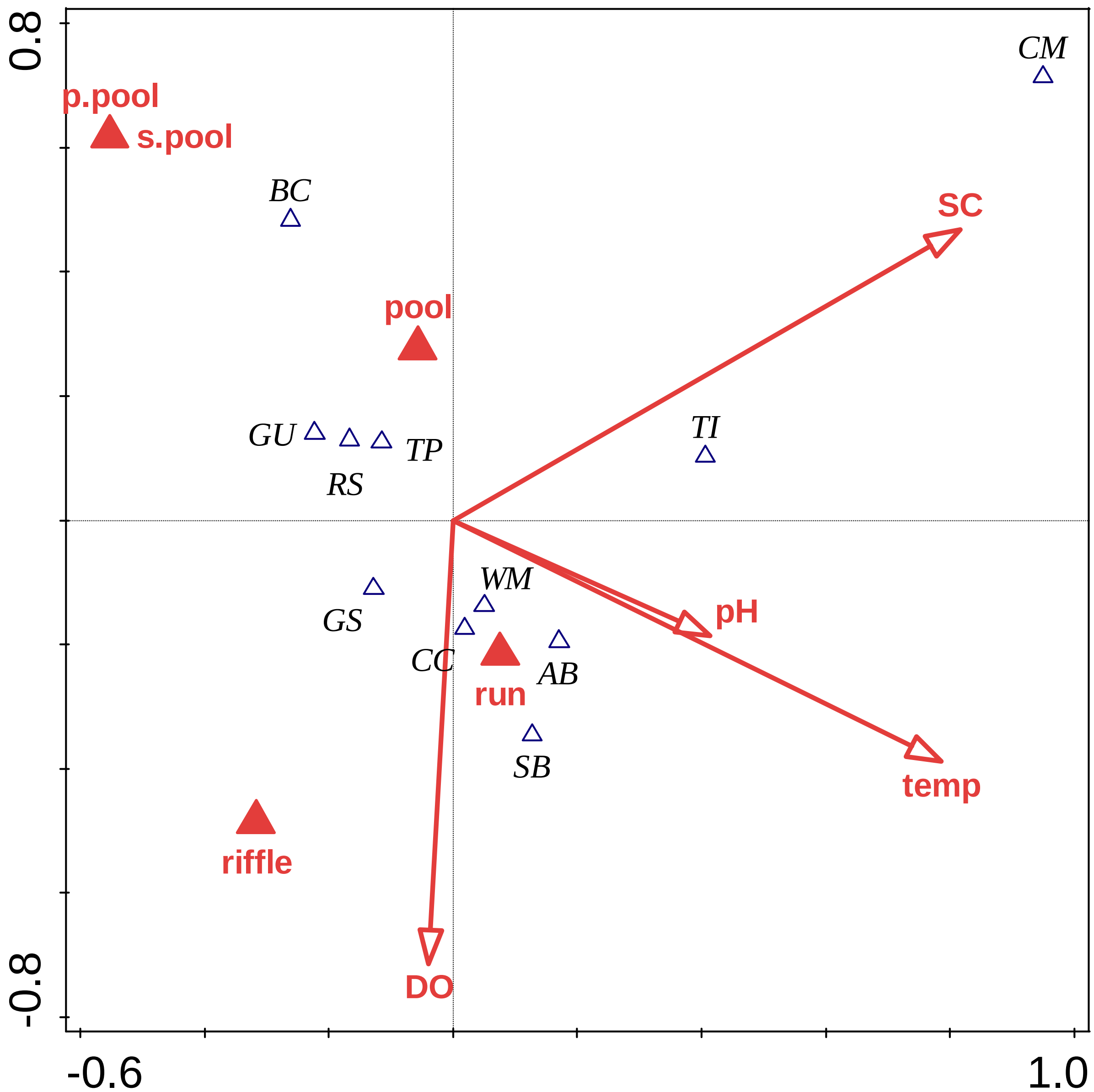


Figure 2.4. Canonical correspondence analysis biplot of taxa composition with in-stream environmental attributes from the presence-absence data subset (64 surveys, 11 taxa, 8 degrees of freedom). The in-stream attributes run, riffle, plunge pool (p.pool), and pool described channel unit. The attributes modified and natural described modified status. The attributes dissolved oxygen, specific conductance, and temperature were abbreviated as DO, SC, and temp, respectively. Taxa codes: GS = Green Swordtail, GU = Guppy, CM = Common Molly, WM = Western Mosquitofish, CC = Convict Cichlid, TI = tilapia, BC = Bristle-nosed Catfish, SB = Smallmouth Bass, TP = Tahitian Prawn, RS = Red Swamp Crayfish, AB = American Bullfrog.

Chapter Three – Characterizing introduced species associations with landscape-scale environmental factors

3.1 Introduction

Patterns in stream environments are largely influenced by natural landscape features, such as topography, climate, and geology (Frissell et al. 1986) and drive the distribution and abundance of associated fauna (Allan 2004). Contemporaneous distribution of stream environments and biota within a catchment are strongly influenced by the interaction between the surrounding drainage area and temporal variability at multiple scales (Allan 2004). However, anthropogenic disturbances such as urbanization and agriculture also influence stream environments by altering riparian vegetation, nutrient and sediment inputs, and hydrologic structure and regimes (Allan 2004). Therefore, both natural and anthropogenic landscape factors strongly influence the baseline of biological potential in streams through their effects on stream environments. The realized biological communities are additionally determined by species dispersal, reproductive success, and biotic interactions such as competition and predation (Poff 1997). This relationship between landscape factors and biotic community was investigated to understand species distributions across large spatial extents (Frissell et al. 1986, Allan 2004). Species associations at the landscape scale have numerous implications for the advancement of stream ecology and management, for example identifying environmental controls on community composition, the most effective scale for stream restoration, and the likelihood of establishment and spread of introduced species (Poff 1997).

The primary objective of Chapter three was to characterize the influence of landscape-scale environmental factors on the distribution of introduced stream species throughout the five main Hawaiian Islands. This assessment described landscape factors that support introduced species and provideded insight into species-specific sources of introductions on the islands. This objective was addressed by assessing biological survey records along with a suite of landscape-scale environmental factors using ordination techniques and an indicator species analysis (Baker & King 2010). The secondary objective of Chapter Three was to investigate the influence of waterfalls on the distribution of introduced stream species. Waterfalls have shown to influence the distribution of native species (McRae et al. 2013), and have been hypothesized to limit the distribution of introduced species (G. Higashi, Hawai'i DLNR, personal communication). The goals of this investigation were to answer the following questions:

(1) Do waterfalls limit the distribution of introduced taxa?
(2) What significant landscape-scale environmental factors characterize the distribution of introduced taxa?
(3) For the significant landscape-scale variables, are natural or anthropogenic factors more important and did taxa exhibit similar associations to landscape factors?

This investigation aimed to inform resource managers of the principal landscape-scale environmental factors that control or influence the distribution of introduced species. Analogous to Chapter Two, but at a landscape-scale that includes reaches, streams, and watersheds, this information served to improve survey efforts intended to detect introduced species, the selection of areas for restoration projects, and evaluations of potential interactions with native species. The results of this chapter complemented Chapter Two, allowing for a multi-scale evaluation of environmental factors that supported introduced species in Hawaiian streams.

3.2 Methods

3.2.1 Attributing biological datasets with the spatial framework

A spatial framework was adopted for this study to conduct landscape-scale analyses. This spatial framework follows an example established for the state of Hawaiʻi by Tingley (2017). This included the Hawaiʻi Fish Habitat Partnership (HFHP) stream layer, a modified version of the 1:24,000 National Hydrography Dataset (NHD 2008; http://nhd.usgs.gov/) designed for an ecologically-based set of spatial units for analysis of Hawaiian streams. Stream segments in the HFHP layer were the basic spatial unit of this framework, and were defined from confluence to confluence, or confluence to a given ecological boundary (i.e., waterfalls, elevation zones, ocean); individual stream segments within this modified hydrography layer were referred to as stream reaches following Wang et al. (2011). All biological and landscape-scale environmental data were associated with individual stream reaches. The HFHP stream layer spans the five main Hawaiian Islands, and included a reach-specific hydrological classification that described reaches as perennial or intermittent.

Survey points were linked to the HFHP stream lines in ArcMap (ESRI 2015) following an established protocol for gathering the National Fish Habitat Partnership dataset (https://ecosystems.usgs.gov/fishhabitat/viewdataset.jsp?sbid=521cd199e4b01458f7857f29). Surveys > 50 m from stream lines were individually assessed for accuracy using survey descriptions, i.e., stream names, and tributary and watershed codes. In cases where the descriptions did not match, surveys were removed. In some cases, two separate surveys were given the same geographic coordinates as a result of GPS failure, e.g., no satellite reception, device malfunction, not recorded, at one of the sites (G. Higashi, Hawaiʻi DLNR, personal communication). If sites had sequential site numbers the sites were kept and assessed as individual sites, if not, the non-sequential site number was removed. This protocol was repeated with the survey effort dataset. Nineteen surveys from the abundance dataset were identified and removed, and 14 surveys from the presence-absence dataset were identified and removed, resulting in a total of 1,965 abundance surveys (7,945 including survey effort) and 452 presence-absence surveys.

3.2.2 Biological data preparation

The biological information used in this landscape analysis was taxon presence-absence at the reach scale, formed through the combination of two datasets that included presence-absence survey dataset from 2008 – 2014, to match the time period of the landscape environmental data, as well as the abundance dataset from 1989 - 2010. Taxa presence for a reach was based on representation in at least one survey, and taxa absence for a reach was based on a lack of representation in surveys (following Steen et al. 2008). Additionally, the survey-effort dataset was used to identify reaches where abundance surveys were conducted, and no introduced species were observed.

Similar to the selection of taxa for the in-stream environmental associations in Chapter Two, taxa were selected from the reach-scale presence-absence dataset (hereafter referred to as reach presence-absence) by weighing management concerns and by data availability. Management concerns were evaluated identically to Chapter Two (see Section 2.2.1). In this assessment, the taxon tilapia was supplemented to include biological information from the tilapia fishes identified at the species level, including Blackchin Tilapia (Sarotherodon melanotheron), Mozambique Tilapia (Oreochromis mossambicus), and Red Belly Tilapia (Tilapia zillii). Data availability was assessed by selecting taxa that occurred in three or more reaches. This process resulted 14 taxa selected (Table 3.1). See Figure 3.1 for a spatial representation of the number of introduced taxa occurrences by reach; see Figures 3.2 – 3.15 for taxa specific reach occurrences.

3.2.3 Assembly of landscape-scale environmental data, and link with spatial framework

Landscape-scale environmental data included both natural and anthropogenic factors assessed at multiple spatial catchments. Three spatial catchments were used to evaluate the landscape characteristics with reference to the HFHP stream layer. (1) Local catchments – catchment boundaries that encompassed landscapes that drained directly to stream reaches (Wang et al. 2011). (2) Upstream catchments – catchment boundaries that encompassed the entire upstream area draining to a specific stream reach. (3) Downstream main channel catchment – catchment boundaries that represented the portion of stream connecting a specific reach to the marine environment.

A suite of natural and anthropogenic landscape and stream network factors known to influence stream community assemblages have been attributed to each reach (Wang et al. 2001, Tingley 2017) and aggregated to upstream and downstream catchments (Tsang et al. 2014, Tingley 2017). Thirty-six natural landscape factors (Table 3.2) described stream size, channel slope, soil characteristics, and rainfall characteristics, and natural landcover (e.g., forest, wetland). Rainfall data were gathered from the Hawaiʻi Rainfall Atlas (Giambelluca et al. 2013), which described annual, dry season (May through October), and wet season (November through April) rainfall characteristics throughout the Hawaiian archipelago from 1978-2007. Soil permeability data were collected from the Soil Survey Geographic Database (NRCS SSURGO; U.S. Department of Agriculture). Land cover data were gathered from the Costal Change Analysis Program (CCAP 2011; National Oceanic and Atmospheric Administration, Office for Coastal Management). To reduce the number of CCAP land cover classifications, three separate classifications for freshwater wetlands were combined (e.g., palustrine forested wetland, palustrine shrub wetland, palustrine emergent wetland), as well as three separate classifications for estuarine wetlands (e.g., estuarine forested wetland, palustrine shrub wetland, estuarine emergent wetland). The remaining natural factors primarily described reach characteristics (e.g., elevation, slope, stream order, etc.) and geological age (Table 3.3).

The eighteen anthropogenic factors (Table 3.4) described human population size, non-natural landcover, stream modifications (e.g., road crossings, ditch intersections, and dams), as well as sources of pollution. Anthropogenic land cover data for impervious surfaces, open development, and agriculture was collected from CCAP. To reduce the number of classifications, the separate classifications "cultivated crops" and "pasture" were combined as agriculture. The remaining anthropogenic factors were assembled and initially assessed by the National Fish Habitat Partnership (Crawford et al. 2016). All anthropogenic factors except 303D, which described streams listed as impaired water bodies under the Clean Water Act, were calculated for all spatial catchments, 303D was calculated for upstream catchment only.

3.2.4 Assessment of waterfalls as barriers to upstream movement

In the Hawaiian Islands, waterfalls are known to influence the species-specific distributions of native stream species based on their ability to climb waterfalls (Keith 2003, Walter et al. 2012). Similarly, waterfalls have been hypothesized to limit the distribution of introduced stream species. However, this has not been investigated due to the complication of undetermined introduction sources and locations. For example, if an introduced species was observed above a waterfall there are two possibilities, the species is able to surpass or climb the waterfall, or the species was introduced above the waterfall. To address this question of whether or not waterfalls are limiting the distribution of introduced species in Hawaiʻi, species presence above waterfalls was assessed, but only for stream reaches upstream of human influences (defined below) which served as an indicator or potential sources of introduction. By ruling out reaches with human influences, the investigation aimed to effectively analyze the capacity of upstream movement of introduces species with respect to differing waterfall heights.

To investigate the influence of waterfalls on the distribution of introduced taxa, locations of waterfalls were assembled from four sources and additional locations were identified with assist of Google Earth Pro (Google Inc. 2017). A waterfall GIS layer was created in a three-step process. Point locations of waterfalls throughout the state were gathered from the National Hydrography Dataset (http://nhd.usgs.gov/), the Hawaiʻi Statewide GIS Program (http://planning.hawaii.gov/gis/), the World Waterfall Database (https://www.worldwaterfalldatabase.com/), and waterfalls identified by Tingley (2017). The stream network within 129 watersheds with biological data were visually inspected for waterfalls using Google Earth Pro (Google Inc. 2017). This included inspecting all main channel reaches downstream of the most upstream biological surveys and reaches immediately upstream of the most upstream biological surveys. Historical satellite imagery (from year 1984 to 2016) was assessed to better identify waterfalls, as different temporal records exhibited various levels of image quality, streamflow amounts, and vegetation coverage. Locations of previously identified waterfalls were inspected for accuracy. Newly identified waterfalls through Google Earth Pro were marked with a point location (e.g., latitude and longitude). Waterfall height, defined as the vertical distance from the top of the waterfall to the bottom of the waterfall, was estimated for all waterfalls using the Path Measure Tool in Google Earth Pro (Google Inc. 2017), which uses the WGS84 EGM96 Geoid. Questionable waterfall identifications and waterfall height estimates were flagged and excluded from the analysis. Estimated waterfall height was then grouped into one of five classes: 0.0 – 5.0 m, 5.1 – 10.0 m, 10.1 – 20.0 m, 20.1 – 30.0 m, and > 30.0 m).

In order to differentiate between species upstream movement and upstream human-facilitated introductions, only stream reaches entirely upstream of human influence were assessed. The level of human influence at a given reach was determined by the two landscape factors, local population density and local road length density (as done by McKinney 2002 and others). For each landscape factor a TITAN analysis was conducted with the selected 14 taxa using reach presence-absence to determine a changing-point that showed an increasing occurrence of introduced taxa. TITAN uses integrated species scores to assess occurrence, abundance, and directionally of taxa responses, which are then used to detect changes in taxa occurrence or abundance along an environmental gradient (Baker & King 2010), see Section 3.2.6 for further description of TITAN. The significant level of human influence represented by each factor were designated as the lowest changing-point of taxa that was both positive (i.e., species presence increased at changing-point) and significant (i.e., exhibited both a 0.95 purity and 0.95 reliability level).

Following the establishment of values that represented human influence (e.g., lowest positive changing-points for population and road length density), and therefore indicated potential human-facilitated introduction, stream reaches without human influence were designated. This was done by selecting reaches with landscape values under the predefined values of human influence, and then by eliminating reaches where upstream reaches exceeded the values of human influence. This resulted in stream reaches that were both free from human influence, and upstream of reaches influenced by human.

These stream reaches were then assessed for locations of biological surveys and waterfalls. For surveys that occurred upstream of waterfalls, the surveys were associated with the maximum waterfall height class that was exceeded. The surveys, and the associated taxa occurrences and maximum waterfall height classes were then assessed collectively to determine if taxa occurred above waterfalls. Lastly, if taxa occurrences were observed above waterfalls in reaches free and upstream of human influence, the presence of agricultural ditches were evaluated as a possible source of taxa introductions.

3.2.5 Identification of the most significant landscape factors

A forward selection CCA was conducted with the selected taxa using reach presence-absence to identify the most significant landscape factors that explained the variation in taxa. Stream reaches that were both upstream of waterfalls and free of human influence, as indicated in the previous section, were excluded from the forward selection CCA. Forward selection CCA is a stepwise ordination technique commonly used in ecological studies to identify a subset of factors explaining variation in a set of dependent variables. Only landscape factors that explained a significant (p value ≤ 0.01) amount of variation in the biological dataset were retained. This analysis was conducted with the CANOCO statistical program (Ter Braak & Smilauer 2012).

Prior to conducting the forward selection CCA, highly correlated landscape factors were identified and removed using a Kendall rank correlation test (Hollander & Wolfe 1973). The Kendall rank correlation is a non-parametric analysis used to estimate a rank-based measure of association between paired variables. The correlation test was conducted using landscape factors linked to reaches with biological survey data. All factors with a Kendall rank correlation coefficient greater than an absolute value of 0.7 were removed (Table 3.5). This test was conducted with the base R Statistical Program (R Core Team 2017). The resulting 96 landscape factors were transformed, so that they were approximately normally distributed to meet the ordination assumptions. Continuous environmental factors were log (x + 0.0000001) transformed, and percentage factors were converted to proportion and then arc-sine square root transformed.

3.2.6 Identification of taxa changing-points for select landscape factors

Taxon-specific responses to landscape factors were assessed using TITAN, a program built to conduct indicator species analysis to examine multiple taxa with a given environmental factor (Baker & King 2010). TITAN improves upon the ecological information provided by the forward selection CCA by individually assessing taxon-landscape responses, providing numerical taxon responses (e.g., changing-points), and improved assessments of uncertainty via bootstrapping. TITAN uses integrated species scores to assess occurrence, abundance, and directionally of taxa responses, which are then used to detect changes in taxa occurrence or abundance along an environmental gradient (Baker & King 2010). TITAN works by combining change-point analysis, used to evaluate community thresholds, with a taxon-specific score implemented in indicator species analysis. Change-point analysis (Qian et al. 2003) is a nonparametric technique that orders and partitions community-level response scores along an environmental gradient, identical to a single-split, multivariate regression tree analysis. Change-point analysis asses the uncertainty associated with the observed change-point using a bootstrap resampling procedure. TITAN replaces the community-level response scores used in change-point analysis with taxon-level response scores from indicator species analysis (Dufrene & Legendre 1997). Indicator species analysis is used to identify indicator taxa in noisy biological data, optimize the number of groups in hierarchical cluster analysis, or evaluate sampling unit groupings on species distributions (Baker & King 2010).

TITAN analyses were conducted for selected taxa using reach presence-absence along with the selected landscape factors associated with those reaches. Similar to the forward selection CCA, stream reaches that occurred above waterfalls and free of human of human influence, as indicated in the Section 3.24, were excluded from the TITAN analyses. Furthermore, reach elevation via minimum reach elevation (L_MinEle) was evaluated in addition to the forward selection CCA results, given the reported importance of this factor on introduced stream species by Brasher et al. (2006). For each analysis, a 250 permutation procedure and a 500 bootstrapping procedure were implemented. The TITAN analyses were conducted using the TITAN2 package (Baker et al. 2015) in the statistical program R. The bootstrap procedure produced two diagnostic indices, purity and reliability, for measuring the quality of the taxon's response. Purity evaluated the direction of the taxon response (e.g., an increase or decrease of taxon presence at the changing-point), while reliability estimated the consistency of *p* values. Only taxa responses that exhibited both a 0.95 purity and 0.95 reliability level (mean proportion of p values ≤ 0.05) were considered significant response for the environmental changing-point. Significant taxa responses were indicated with a z score which represented the relative magnitude of change and sensitivity to the gradient (Baker & King 2010). Taxon-specific responses were visualized using a TITAN plot for each landscape factor, where response direction was indicated by color, the changing-point value was indicated by symbols (sized in proportion to z scores), and horizontal lines overlapping each symbol represented the 5^{th} and 95^{th} percentiles among bootstrap replicates.

3.3 Results

3.3.1 Waterfall assessment

TITAN analyses were conducted to identify the potential thresholds of anthropogenic landscape factors that represented sources of species introductions. The results indicated that the presence of introduced species increased when local population density exceeded 4.24 people/km^2 (Table 3.6) and when local road length density exceeded 0.01 km/km^2 (Table 3.7). Green Swordtail exhibited the lowest significant environmental changing-point for local population density and Western Mosquitofish exhibited the lowest significant environmental changing-point for local road length density. These thresholds were used to exclude stream reaches that were subject to anthropogenic influences, i.e., acting as potential anthropogenic sources of introductions of non-native species**.**

After identifying stream reaches without human influence and therefore potential anthropogenic introduction sources, the number of biological surveys located within these reaches for each island were: 343 for Kauaʻi, 408 for Oʻahu, 612 for Molokaʻi, 662 for Maui, and 141 for Hawaiʻi (Table 3.8). See Table 3.8 for an island-specific distribution of these biological surveys with respect to the predefined waterfall height classes.

Of the 14 taxa evaluated, taxa were absent in reaches above any waterfall, with the exception of Tahitian Prawn and American Bullfrog (See Table 3.9 for a summary of all taxa occurrences with respect to waterfall height classes). Within all islands evaluated, Tahitian Prawn occurred in 390 surveys entirely upstream of human influence, of these surveys 27 occurred above 0.0-5.0 m falls (located in three streams, two on Molokaʻi and one on Maui), three occurred above 10.1-20.0 m falls (within one stream on Maui), and four occurred above 20.1-30.0 m falls (within one stream on Kauaʻi). American Bullfrog occurred in seven surveys entirely upstream of human influence, of these surveys three occurred above 10.0-20.1m falls, located in one stream on the island of Hawaiʻi. For the two taxa that occurred above waterfalls in areas upstream of human influence, agricultural ditches did not intersect any of the upstream connecting reaches, which excludes the potential of agricultural ditches to serve as introduction paths. Forty-nine reaches that were found to be both upstream of human influence and upstream of waterfalls were excluded from the following analyses (e.g., forward selection CCA and TITAN), due to these reaches being inaccessible for the majority of taxa investigated.

3.3.2 Forward selection CCA

The forward selection CCA conducted using reach presence-absence and the associated landscape factors (14 taxa, 591 reaches) indicated that the 21 significant ($p \leq 0.01$) environmental factors explained 26.2% of the total variation in taxa (Table 3.10, Figure 3.16), the first four axes cumulatively explained 8.42, 13.04, 16.85, and 19.81% of the total variation. Significant landscape factors, such as upstream mean annual rainfall, downstream channel slope, upstream population density, and upstream road length density, were kept for CCA analysis. Correlated landscape factors, including those retained and excluded in the CCA analysis are listed in Table 3.5.

Visual inspection of the forward selection CCA biplot (Figure 3.16) indicated that downstream mean and maximum channel slope upstream mean and maximum rainfall, and upstream mean air temperature strongly influenced the variation in taxa compositional along the primary axis. Along this axis, the slope and rainfall factors occurred in the opposite direction of many of the anthropogenic factors (e.g., upstream population density and upstream road length density among others). Most taxa occurred in the direction of increasing anthropogenic factors, the taxa tilapia and to a lesser extent, the Smallmouth Bass, occurred with the highest level of anthropogenic factors. Tahitian Prawn was the only taxon that occurred in the direction of increasing rainfall and slope factors. Variation along the secondary axis was primarily influenced by local percent open water and upstream maximum soil permeability, which occurred in the same direction. Along this gradient, Smallmouth Bass and tilapia occurred in in the direction of increasing open water and upstream maximum soil permeability, while the remaining taxa occurred around the center of the plot or marginally in the opposite direction.

3.3.3 TITAN analysis

Only taxa that exhibited significant responses (i.e., both a 0.95 purity and 0.95 reliability level) with landscape factors were reported (see Table 3.11 for a summary of taxa responses). A positive response indicated that the presence of a taxa increased at a given environmental changing-point (env.cp), and conversely a negative response indicated that the presence of a taxa decreased at a given environmental changing-point. Each significant environmental changing-point (env.cp) was associated with a z score (z) that represented the relative magnitude of change or sensitivity to the environmental gradient. The associated uncertainty values and non-significant taxa results can be found in the corresponding supplemental tables (Tables S 3.1 to S 3.22).

The TITAN analyses conducted with the selected taxa using reach presence-absence and the selected 22 landscape factors (Figures 3.17 to 3.35) found that landscape factors with the greatest number of significant changing-points among taxa included the natural factors downstream channel slope

(D_Slope; Figure 3.17), downstream maximum channel slope (D_MaxSl; Figure 3.18), upstream mean annual rainfall (U_MeanAnnRain; Figure 3.19), upstream maximum annual rainfall (U_MaxAnnRain; Figure 3.20), reach elevation (L_MinEle; Figure 3.21), upstream mean air temperature (U_MeanTemp; Figure 3.22), local percent open water (L_OpWater; Figure 3.23), and the anthropogenic factors upstream population density (U_Pop; Figure 3.30), upstream road length density (U_RoadLen; Figure 3.31), and downstream ICIS sites (D_ICIS; Figure 3.32).

For the prominent natural factors, downstream channel slope (D_Slope; Figure 3.17) exhibited a negative effect on Green Swordtail (env.cp = 4.06), Guppy (env.cp = 3.64), Common Molly (env.cp = 2.51), Western Mosquitofish (env.cp = 4.45), tilapia (env.cp = 0.57), and Convict Cichlid (env.cp = 2.06). Downstream maximum channel slope (D_MaxSl; Figure 3.18) exhibited a negative effect on Green Swordtail (env.cp = 9.87), Guppy (env.cp = 9.72), Common Molly (env.cp = 3.45), Western Mosquitofish (env.cp = 9.87), tilapia (env.cp = 0.86), Convict Cichlid (env.cp = 3.30), and Tahitian Prawn (env.cp = 12.78). Upstream mean annual rainfall (U_MeanAnnRain; Figure 3.19) exhibited a negative effect on Green Swordtail (env.cp = 5000.34), Common Molly (env.cp = 3393.25), Western Mosquitofish (env.cp = 2373.48), tilapia (env.cp = 2789.85), and a positive effect on Tahitian Prawn (env.cp = 2472.56). Upstream maximum annual rainfall (U_MaxAnnRain; Figure 3.20) exhibited a negative effect on Western Mosquitofish (env.cp = 3886.34), tilapia (env.cp = 1603.25), and Red Swamp Crayfish (env.cp = 2542.87), and a positive effect on Guppy (env.cp = 8920.75) and Tahitian Prawn (env.cp = 2858.53). Minimum Reach elevation (L_MinEle; Figure 3.21) exhibited a negative effect on Green Swordtail (env.cp = 209.00), Guppy (env.cp = 229.00), Common Molly (env.cp = 28.00), Western Mosquitofish (env.cp = 209.00), tilapia (env.cp = 3.00), and Tahitian Prawn (env.cp = 80.00). Upstream mean air temperature (U_MeanTemp; Figure 3.22) exhibited a positive effect on Green Swordtail (env.cp = 20.62), Guppy (env.cp = 20.62), Common Molly (env.cp = 21.61), Western Mosquitofish (env.cp = 22.95), tilapia (env.cp = 23.65), and Convict Cichlid (env.cp = 21.90). Local percent open water (L_OpWater; Figure 3.23) exhibited a negative effect on Green Swordtail (env.cp = 0.00), Guppy (env.cp = 0.06), Western Mosquitofish (env.cp = 0.00), Tahitian Prawn (env.cp = 4.39), Red Swamp Crayfish (env.cp = 0.03), and a positive effect on tilapia (env.cp = 0.10).

For the prominent anthropogenic factors, upstream population density (U_Pop; Figure 3.30) exhibited a positive effect on Green Swordtail (env.cp = 3.76), Guppy (env.cp = 4.17), Common Molly (env.cp = 25.68), Western Mosquitofish (env.cp = 23.14), tilapia (env.cp = 131.09), Convict Cichlid (env.cp = 40.86), and Red Swamp Crayfish (env.cp = 516.61). Upstream road length density (U_RoadLen; Figure 3.31) exhibited a positive effect on Guppy (env.cp = 7.08), Common Molly (env.cp = 0.21), Western Mosquitofish (env.cp = 1.67), tilapia (env.cp = 2.26), American Bullfrog (env.cp = 0.41), Red Swamp Crayfish (env.cp = 6.73), and a negative effect on Tahitian Prawn (env.cp = 2.29). Downstream ICIS site density (D_ICIS; Figure 3.32) exhibited a positive effect on Green Swordtail (env.cp = 0.23), Guppy (env.cp = 1.05), Western Mosquitofish (env.cp = 0.47), tilapia (env.cp = 0.12), and a negative effect on Tahitian Prawn (env.cp = 0.00).

3.4 Discussion

This study examined landscape-scale associations of introduced stream species throughout the five main Hawaiian Islands by evaluating the influence of waterfalls as natural barriers to upstream movement, as well as the most influential landscape factors to species distributions, including the associated taxon-specific changing-points. Waterfalls were found to limit the upstream distribution of introduced taxa with the exception of Tahitian Prawn and American Bullfrog which were found to occur upstream of waterfalls, in locations with minimal human influence (e.g., based on density of human populations and roads). Furthermore, both natural and anthropogenic landscape factors significantly influenced the distribution of taxa, the landscape factors with the greatest number of significant changing-points among taxa included downstream slope, upstream rainfall, elevation, population density, and road length density among others. Upstream rainfall, downstream slope, and elevation generally limited the distribution of introduced species, i.e., species presence decreased at a point along the environmental gradients, while population density and road length density were associated with the increased presence of introduced species.

3.4.1 Waterfall as barriers to upstream movement

The waterfall assessment indicated that Tahitian Prawn and American Bullfrog occurred above waterfalls in areas upstream of human influence. Both species occurred above 20.1-30.0m waterfalls in one stream per species, and the Tahitian prawn was additionally found above smaller falls including three streams above 0.0-5.0m falls, and one stream above 10.1-20.0m falls. This finding supported previous accounts of the suspected climbing ability of Tahitian Prawn (Yamamoto & Tagawa 2000) and was not surprising given the ability of the American Bullfrog to temporarily move over land (Gahl et al. 2009). There was inadequate evidence to determine a limiting waterfall height for either species, but the number of surveys above different waterfall height categories in the assessment suggested that Tahitian Prawn was more able to surpass smaller waterfalls (0.0-5.0m) compared to larger waterfalls (10.0-30.0m). In this study, no adequate conclusion was drawn for American Bullfrog. Yet, previous studies on the American Bullfrog have shown that the species dispersal abilities were enhanced in wetter areas, as moisture is required for substantial dispersal (Smith & Green 2005, Gahl et al. 2009). Additionally, major agricultural ditches have been suspected as a potential means for the movement of introduced species between watersheds, however, in this assessment ditches did not intersect streams upstream of taxa occurrences (when they occurred above waterfalls). Although, given the small number of reaches assessed, there was inadequate evidence to determine the effect of agricultural ditches on the dispersal of introduced species.

While this assessment served as a preliminary investigation, and only evaluated stream with biological surveys with introduced species, there were apparent trends in the number and types of waterfalls among islands. Hawaiʻi Island and Maui both exhibited the greatest number of waterfalls. Additionally, the terminal waterfalls, which, occurred at the coastline and terminated in the ocean, were only observed on these two islands. Terminal waterfalls may inhibit the dispersal of introduced species to stream system that are able to disperse through marine environments (Nico & Walsh 2011), such as the Tahitian Prawn (Yamamoto & Tagawa 2000) and Blackchin Tilapia (Brown et al. 1999).

Although not adequately represented in this assessment, suckermouth catfishes (family *Loricariidae*, including the species Bristle-nosed Catfish and Armored Catfish) have been reported to surpass small (1.0-2.0m) waterfalls and move upstream moderate distances. For example, after the restoration of a weir in Waihee Stream on Oʻahu for native fish passage which provided a 1.0-2.0m near-vertical surface for native species to climb (removing an overhung lip which deterred native species passage), both native fishes and introduced Bristle-nosed Catfish were observed above the structure where they were previously not found (Glenn Higashi, Hawaiʻi DLNR, personal communication).

Additionally, biologist Cory Yap has observed Bristle-nosed Catfish in the upper reaches of Helemano Stream on Oʻahu at approximately 2100.0 m elevation, which indicated the species ability to move upstream as this area was uninhabited.

3.4.2 Landscape associations

The CCA conducted with the taxa using reach presence-absence indicated that anthropogenic landscape factors were strongly associated with each other, as well as all the introduced taxa assessed apart from the Tahitian Prawn. These reaches with introduced taxa and anthropogenic factors were characterized by the natural landscape factors: low upstream rainfall and downstream channel slope, and high mean air temperature (via the upstream catchment). The association of most of the taxa with anthropogenic factors reflected the human-facilitated introductions of taxa, however, species-specific responses to landscape factors were investigated with TITAN to better understand differences in the distributions among taxa.

Among the natural landscape factors assessed, factors that exhibited the greatest number of significant changing-points among the selected taxa were upstream rainfall (including mean annual and maximum annual), downstream slope (including mean and maximum), and elevation. An increase in these factors were associated with decreased presence of introduced taxa, therefore acting as limiting factors on taxa distributions. Additionally, the landscape factors local percent open water, which represented stream channel width, associated with a decrease in taxa occurrence.

Upstream rainfall and downstream channel slope were likely representing natural landscape factors that limit the environemntal suitability and upstream movement of introduced stream species. As upstream annual rainfall increases, it is expected that the frequency and magnitude of high flow events would correspondingly increase (Oki et al. 2010). These disturbance events can cause mortality or displace species downstream, as well as alter local ecosystem characteristics including physical (e.g., hydrological and substrate characteristics) and biological factors (e.g., epiphyton, benthic invertebrate communities, and terrestrial inputs; Fitzsimons et al. 1997). In Hawaiʻi, poeciliid fish densities have been reported to decrease during the wet season compared to dry season densities (Holitzki et al. 2013), which likely resulted from increased magnitude and frequency of high flow events. In our study, increased upstream mean annual rainfall was associated with the decreased occurrence of Green Swordtail, Common Molly, Western Mosquitofish, and tilapia, which may indicate that these taxa cannot withstand the streamflow conditions characteristic of high-rainfall areas. On the other hand, Tahitian Prawn occurrence increased with upstream mean annual rainfall, which supported the theory that this species can tolerate flashy streamflow conditions similar to native species (Yamamoto & Tagawa 2000). This response was consistent with the finding in the assessment of in-stream environments (Chapter Two) where Tahitian Prawn was associated with bedrock substrate that may have indicated higher-elevation locations and the potential of frequent high streamflow events (Seidl et al. 1994). The effects of upstream maximum rainfall on taxa were consistent with upstream mean annual rainfall for taxa with significant responses. However, Guppy occurrence increased with relatively high levels of upstream maximum rainfall (8920.75 mm/yr). Similar to the Tahitian Prawn, this response corresponded to the finding in the assessment of in-stream environments (Chapter Two) where Guppy was associated with bedrock habitats that possibly indicated the frequent occurrence of high streamflow events.

Similar to upstream rainfall, stream channel slope likely limited the environmental suitability and upstream movement of introduced stream species. Channel slope influences the hydrologic characteristics of stream environments, particularly, streamflow velocity and the induced turbulence, which are generally thought to be unfavorable conditions for introduced species (Brasher et al. 2006). In this assessment, downstream channel slope and downstream maximum channel slope exhibited similar patterns among taxa responses, with the magnitude of changing-points for downstream maximum slope exceeding the changing-points of downstream slope. Downstream maximum channel slope served as a more informative factor for taxa distributions, as taxa changing-points could be interpreted as the approximate channel slope limitations for each taxon. Guppy and Tahitian Prawn exhibited the highest channel slope limitations, which may indicate the taxa's ability to be more tolerant of hydrologically dynamic stream environments.

Reach elevation, indicated by minimum reach elevation, exhibited negative effects on all taxa with significant responses. Tilapia and Common Molly were limited to the lowest elevations (3.0m and 28.0m, respectively), followed next by Tahitian Prawn which decreased above 80.0m elevation. While the three poecilids Green Swordtail, Guppy, and Western Mosquitofish exhibited the largest elevation range, which all decreased around 220.0m elevation. These findings were consistent with to the previous assessment of in-stream environments (Chapter Two) in which tilapia and Common Molly were associated with high temperature and high specific conductance environments, which are typically associated with low-elevation coastal streams. While Tahitian Prawn, Guppy, and Green Swordtail were associated with habitat attributes characteristic of higher-elevation mountainous streams (e.g., cooler, deeper waters, with boulder and bedrock substrates). Overall, the responses indicated that all taxa generally occurred at low elevations, however, some taxa exhibited larger elevation ranges, and therefore may pose greater impacts to native stream species.

In this study, elevation was likely representing multiple natural and anthropogenic landscape factors which influence the distribution of introduced species, through both effects on stream environments and by sources of introductions. For example, rainfall and channel slope typically increase as elevation increases, while air temperature and water temperature typically decrease as elevation increases. This results in higher elevation streams being characterized by increased streamflow velocity and turbulence, and cooler streams that are more prone to flashy streamflow conditions. Whereas, human populations, roads, and other sources of development occur most frequently at lower elevations (Brasher et al. 2006), where they serve as sources of species introductions and environmental degradation. For example, in Hawaiʻi the majority of streams in urban areas have been channelized for flood control and road crossings (Brasher et al. 2006). This interaction between the distribution of introduced stream species and elevation throughout the state of Hawaiʻi was previously investigated by Brasher et al. (2006) which similarly found introduced species primarily occurred at lower elevations.

Other natural landscape factors with a notable number of significant changing-points among taxa included local percent open water, which represented stream channel width. Stream reaches classified with high percentages of open water were primary lower elevation coastal reaches (i.e., estuarine areas), and secondarily streams with large pools typically found immediately downstream of waterfalls. Tilapia exhibited a positive response to open water, which corresponds to the taxon's use of low elevation stream reaches identified in this study. The taxa Green Swordtail, Guppy, Western Mosquitofish, Red Swamp

Crayfish, and Tahitian Prawn exhibited a negative response to open water which indicated a preference for smaller streams or an avoidance of coastal stream reaches.

Of the anthropogenic landscape factors assessed, those that exhibited the greatest number of significant changing-points among the selected taxa were upstream population density, upstream road length density. Upstream population density, which was strongly correlated with local population density, was related to the increased occurrence of Red Swamp Crayfish, tilapia, Convict Cichlid, Western Mosquitofish, Common Molly, Guppy, and Green Swordtail. All of the taxa were associated with high population densities, however, poeciliid fishes (including Common Molly, Guppy, Green Swordtail, and Western Mosquitofish) exhibited the widest association with population densities as they were found to increase after low densities (approximately 3-20 people per km^2) were exceeded. Whereas, the Convict Cichlid and tilapia exhibited associations with population density when higher densities occurred (40 people per km^2 and 130 people per km^2, respectively). The differing responses of these fishes to population densities reflected their introduction sources. Poeciliid fishes such as Guppy, Western Mosquitofish, and Green Swordtail were widely and intentionally stocked in various freshwater habitats (e.g., streams, ponds, reservoirs, ditches) in urban, agricultural, and remote areas for mosquito control throughout Hawaiʻi (Yamamoto & Tagawa 2000, Brasher et al. 2006), which reflected the fishes increased occurrence with the widest range of population densities. Convict Cichlid has been introduced by amateur aquarium owners (Yamamoto & Tagawa 2000, Brasher et al. 2006), which have been associated with more populated areas (e.g., residential areas), and thus corresponds to increased occurrence after larger populations were exceeded. While tilapia, which occurred with even higher population densities, corresponded with the documented introduction of these fishes for commercial purposes (e.g., bait fish, aquaculture; Yamamoto & Tagawa 2000) which are associated with dense human populations in urban areas.

The significance of the upstream catchment of population density, rather than the downstream catchment, given that the majority of human populations in Hawaiʻi reside along the coast (i.e., downstream areas; Brasher et al. 2006), indicated that the introduced species assessed here were more likely to reside locally or downstream of the location where they were introduced. The upstream movement of introduced species have likely been impeded by natural gradients (e.g., increasing rainfall and channel slope that create dynamic and challenging stream environments) or barriers including waterfalls, dams, and diversions. However, the Tahitian Prawn and American Bullfrog did not exhibit a significant environmental changing-points for upstream population density which may have reflected the taxa's ability for greater dispersal. The Tahitian Prawn has been documented to disperse to new watersheds through marine environments without human-mediated intervention, via the taxon's amphidromous lifecycle (Yamamoto & Tagawa 2000). While the American Bullfrog has been reported to moveshort distances over land and further distances if utilizing wetted areas (e.g., ponds, swamps, and agriculture ditches; Smith & Green 2005, Snow & Witmer 2010).

Upstream road length density exhibited similar taxa responses as population density, which corresponds to areas with high population densities having high road length densities. Additionally, upstream road length density indicated the level of human influence in areas outside of populated areas (e.g., traffic and recreational activities outside of urban and residential areas). The decreased occurrence of Tahitian Prawn with low levels (e.g., 2.3 km/km^2) of upstream road length densities indicated that the species was negatively affected by increased human access. This may represent the species inability to tolerate the stream alterations associated with roads (e.g., channelization) or it may represent increased accessibility for people targeting these prawns for food (Bob Kinzie, personal communication).

The landscape associations exhibited by taxa in this study are likely not directly comparable to species native ranges due to large differences in stream environments, and the potential of adaptive evolution and hybridization. In many cases, Hawaiian streams exhibit unique characteristics including small, steep, and flashy, which are different from continental streams. For example, in a landscape assessment of fish assemblages that included Western Mosquitofish within a portion of its native range (i.e., Oklahoma, USA), average channel slopes varied between 0.5% (with a standard deviation of 0.4%) and 0.7% (with a standard deviation of 0.6%; Dauwalter et al. 2008). Whereas in Hawaiʻi, the range of channel slopes far exceed those of the studied native range, and Western Mosquitofish occurred until downstream channel slopes exceeded approximately 5.0% slope. Additionally, it is possible that introduced species have adapted to Hawaiian streams, and the populations in Hawaiʻi may have different traits compared to their native-range populations. Guppies and other poeciliids have exhibited differential traits (e.g., morphology, life history, and behavior) in response to predator intensity (Magurran 2005), which has generally been associated with changes in stream environments that occur from headwaters to lower reaches (Endler 1995, Carmona-Catot et al. 2011, Torres Dowdall et al. 2012). Furthermore, the tilapia species that occur in Hawaiʻi have been documented to hybridize with each other (Yamamoto & Tagawa 2000), which may result in differential traits relative to the pre-hybridized species.

While the landscape associations observed here may not be comparable to the species native ranges (e.g., continental streams), they may serve as a model of landscape associations for introduced taxa on other tropical islands. The landscape associations identified in this study may inform other tropical islands of areas generally suitable for introduced stream species and may potentially indicate problematic species (i.e., those that have the greatest distributions). Additionally, the extent of development and population densities found in Hawaiʻi, and their relationship with introduced species, including introduction sources and environmental degradation, may serve as an example for less disturbed islands.

3.4.3 Future directions

The best actions to advance the understanding and management of introduced species in Hawaiʻi included surveying underrepresented areas, systematically repeating surveys through time, developing species removal strategies, and enacting public involvement through education. In this study, the major areas underrepresented by biological surveys included areas upstream of human influences, agricultural ditches, reservoirs, and urban areas, furthermore, surveys in estuaries would make the monitoring more complete. Collectively, biological information from these areas would greatly improve the understanding of introduced species distributions and dispersal abilities. Surveys in areas upstream of human influences would provide important information on the capacity for various species upstream movement. Surveys conducted in agricultural ditches would investigate the capacity of the lateral movement of species between watersheds. Whereas surveys in reservoirs could indicate source populations for some species. Surveys in urban areas, which are uncommon due to water quality concerns as well as decreased native species and environmental quality, could indicate the early presence of highly invasive species allowing for rapid response control measures.

In addition to sampling underrepresented areas, the systematic re-surveying locations assessed in this study would provide an indication of how the distribution and population sizes of these species are changing through time. This will be important given that climate change is expected to alter the timing and amount of rainfall in Hawaiʻi, and therefore our streamflow (Zhang et al. 2016). Oki (2004) reported that base streamflow decreased throughout the state from 1913 to 2002, which corresponds with the long-term downward trend in annual rainfall amounts. Decreased streamflow would result in decreased habitat availability and increased stream temperatures (Brasher 2003), the former would result in increased competition between native and introduced species for space and food. Another type of sampling that would be beneficial to the management of introduced species are surveys conducted following very large storm events, as this would provide information on the tolerance of various species to duration, frequency and magnitude of floods, as long if monitoring occurs before the flood in order to establish a baseline.

3.5 Conclusion

In this assessment, the significance of select natural landscape factors, including upstream rainfall and channel slope, likely represented natural barriers to species ranges through their effect on stream hydrology which creates unfavorable streamflow conditions for introduced species. While the significance of select anthropogenic landscape factors, including population density and road density likely represent areas of high human influence which corresponded to both to sources of species introductions and stream degradation. Both of these effects promote the prevalence of introduced species in stream ecosystems, in addition to negatively influencing native stream species. Elevation was found to encompass the effects of both natural factors that prevent species from higher elevations, and anthropogenic factors which contributed to sources of introductions and stream degradation at lower elevations.

For taxa with significant landscape associations, taxa occured primarily in stream reaches under 200m elevation and with channel slopes less than 8%. The majority of these taxa were associated with human populations, roads, and other indicators of human development (e.g., downstream ICIS sites). While this response to anthropogenic factors represented a tolerance to degraded stream conditions, it showed the influence of introduction sources on the taxa's distributions. Species that were introduced for mosquito control (e.g., Guppy, Western Mosquitofish, Green Swordtail) were associated with a wider range of population sizes, whereas species introduced by amateur home aquarium owners (e.g., Convict Cichlid) and commercial operations (e.g., tilapia) were associated with larger human populations.

There were apparent trends among the responses of taxa to various natural and anthropogenic landscape factors. However, many taxa exhibited unique responses which indicated differential associations with these landscape factors. Tahitian Prawn exhibited the most substantial differences as the species was associated with more natural and dynamic streams, and an avoidance of human-influenced streams. This likely represented the species natural ability to disperse to new stream systems, the negative responses to human influences may have represented an intolerance to stream alterations, increased access for fishing, or a disruption of the stream-ocean connectivity required for reproduction. Tilapia exhibited responses on the opposite side of the spectrum, as it occurred at the lowest elevations and channel slopes, and with greater levels of anthropogenic disturbances. This agreeed with the previously documented lower stream occurrence (Englund et al. 2000) and indicated that the taxon is particularly tolerant of the stream alterations that are characteristics of dense human populations. Additionally, both Tahitian Prawn and American Bullfrog exhibited the ability to move upstream of waterfalls.

The management of introduced freshwater species is critical for the conservation of native stream species as well as native waterbirds and marine species that utilize estuarine areas of streams. Although the management of freshwater ecosystems has been greatly underfunded compared to marine and terrestrial systems in Hawaiʻi, stream ecosystems serve as an integral linkage to connect marine and terrestrial ecosystems, and therefore require attention to ensure the holistic conservation and protection of ecosystems. Future research that would greatly improve the management of introduced stream species in Hawaiʻi include the documentation and description of waterfalls (e.g., both natural waterfalls and dams) and stream diversions, as these may influence the movement of introduced species. Further implementation of biological surveys conducted both in areas previously surveyed as well as areas underrepresented by biological survey (e.g., areas upstream of human influences, agricultural ditches, reservoirs, urban areas, and estuarine areas) would support information regarding changes in species population sizes and ranges, in addition to the early detection of newly introduced species.

Chapter Three Tables

Table 3.1. Taxa selected for landscape-scale analyses using reach presence-absence. Taxa information were summarized by total number of unique reach occurrences, and the number of unique reach occurrences by island. Code indicated the two-letter taxon identifier used for analyses.

Scientific Name	Common Name	Code	Total Number of Reach Occurrences					
			All islands	Hawai'i	Kaua'i	Maui	Moloka'i	O'ahu
Ancistrus cf. temminckii	Bristle-nosed Catfish	BC	4	-	-	-	-	4
Archocentrus nigrofasciatus	Convict Cichlid	CC	7	-	2	-	-	5
Gambusia affinis	Western Mosquitofish	WM	65	16	26	7	-	16
Limia vittata	Cuban Limia	CL	4	-	-	-	-	4
Macrobrachium lar	Tahitian Prawn	TP	246	82	30	49	31	54
Micropterus dolomieu	Smallmouth Bass	SB	4	-	4	-	-	-
Micropterus salmoides	Largemouth Bass	LB	4	-	4	-	-	-
Misgurnus anguillicaudatus	Pond Loach	PL	7	4	-	-	-	3
Poecilia reticulata	Guppy	GU	77	15	13	22	-	27
Poecilia sphenops	Common Molly	CM	11	1	2	1	-	7
Procambarus clarkii	Red Swamp Crayfish	RS	20	5	7	6	-	2
Rana catesbiana	American Bullfrog	AB	26	6	12	5	-	3
Tilapiini (*Cichlidae*) spp.	Tilapia	TI	27	-	15	-	-	12
Xiphophorus helleri	Green Swordtail	GS	87	8	18	13	-	48

Table 3.2. Natural landscape factors initially assessed in the landscape-scale analysis. Catchment of landscape summary: (L) local, (U) upstream, (D) downstream.

Code	Factor Description	Catchment	Unit	Resolution	Source
DistInl	Reach distance inland	L	m	1:24,000	HFHP[1]
Slope	Reach slope	L, U, D	%	10m	HFHP[1], NED[2]
DMaxSl	Downstream maximum slope	D	%	10m	HFHP[1], NED[2]
MinEle	Minimum reach elevation	L	m	10m	HFHP[1], NED[2]
MaxEle	Maximum reach elevation	L	m	10m	HFHP[1], NED[2]
MpEle	Midpoint reach elevation	L	m	10m	HFHP[1], NED[2]
Order	Stream order	L	.	.	HFHP[1]
Erod	Soil erodibility	L, U	.	1:12,000 - 1:63,360	SSURGO[3]
Geo	Geologic age	L, U	.	.	USGS[4]
SolRad	Solar radiation	L, U	cal/cm^2	.	Hawaiʻi OP[5]
MeanTemp	Mean air temperature	L, U	°C	800m	PRISM[6]
MaxTemp	Maximum air temperature	L, U	°C	800m	PRISM[6]
MinTemp	Minimum air temperature	L, U	°C	800m	PRISM[6]
Area	Catchment area	L, U, D	km^2	1:24,000	HFHP[1], NED[2]
MeanAnnRain	Mean annual rainfall	L, U	mm/yr	250m	HRA[7]
MeanDryRain	Mean dry season rainfall	L, U	mm/yr	250m	HRA[7]
MeanWetRain	Mean wet season rainfall	L, U	mm/yr	250m	HRA[7]
MaxAnnRain	Maximum annual rainfall	U	mm/yr	250m	HRA[7]
MinAnnRain	Minimum annual rainfall	U	mm/yr	250m	HRA[7]
RanAnnRain	Range mean of annual rainfall	U	mm/yr	250m	HRA[7]
StdAnnRain	Standard deviation of annual rainfall	U	mm/yr	250m	HRA[7]
SumAnnRain	Total amount of annual rainfall	U	mm/yr	250m	HRA[7]
MeanSoilPerm	Mean soil permeability	L, U	in/hr	30m	SSURGO[3]
MaxSoilPerm	Maximum soil permeability	L, U	in/hr	30m	SSURGO[3]
MinSoilPerm	Minimum soil permeability	L, U	in/hr	30m	SSURGO[3]
StdSoilPerm	Standard deviation soil permeability	L, U	in/hr	30m	SSURGO[3]
RanSoilPerm	Range soil permeability	L	in/hr	30m	SSURGO[3]
Grass	Percent cover of grassland	L, U, D	%	30m	CCAP[8]
Forest	Percent cover of forest	L, U, D	%	30m	CCAP[8]
Shrub	Percent cover of shrubland	L, U, D	%	30m	CCAP[8]
Barren	Percent cover of barren land	L, U, D	%	30m	CCAP[8]
UncShr	Percent cover of unconsolidated shore	L, U, D	%	30m	CCAP[8]
FrWet	Percent cover of freshwater wetland	L, U, D	%	30m	CCAP[8]
EsWet	Percent cover of estuarine wetland	L, U, D	%	30m	CCAP[8]
FrAqBed	Percent cover of freshwater aquatic bed	L, U, D	%	30m	CCAP[8]
OpWater	Percent cover of open water	L, U, D	%	30m	CCAP[8]

(1) Hawaiʻi Fish Habitat Partnership, USGS, http://assessment.fishhabitat.org/#. (2) National Elevation Dataset, USGS, https://lta.cr.usgs.gov/NED. (3) Soil Survey Geographic Database, NRCS, https://water.usgs.gov/osw/streamstats/. (4) USGS Geologic Map of Hawaiʻi, https://pubs.usgs.gov/of/2007/1089/. (5) State of Hawaiʻi Office of Planning, http://planning.hawaii.gov/. (6) PRISM Climate Data, http://prism.oregonstate.edu/. (7) Hawaiʻi Rainfall Atlas (Giambelluca et al. 2013), University of Hawaiʻi, http://rainfall.geography.hawaii.edu/. (8) Costal Change Analysis Program, NOAA, https://coast.noaa.gov/digitalcoast/tools/lca.

Table 3.3. Geologic age group classification, ka = thousand years, Ma = million years (Sherrod et al. 2007).

Code	Age Range
1	Sedimentary rocks and deposits that span several age ranges
2	0-200 yr
3	200-750 yr
4	750-1,500 yr
5	1,500-3,000 yr
6	3,000-5,000 yr
7	5,000-10,000 yr
8	10-30 ka
9	30-50 ka
10	50-140 ka
11	140-780 ka
12	780-1,000 ka
13	1-2 Ma
14	2-4 Ma
15	4-6 Ma

Table 3.4. Anthropogenic landscape factors initially assessed in the landscape-scale analysis. Catchment of landscape summary: (L) local, (U) upstream, (D) downstream.

Code	Factor Description	Catchment	Unit	Scale	Year of the dataset	Source
Pop	Population density	L, U, D	#/km^2	1:100,000	2010	TIGER Census[1]
ImpSur	Percent cover of impervious surfaces	L, U, D	%	30m	2011	CCAP[2]
OpDev	Percent cover of open development	L, U, D	%	30m	2011	CCAP[2]
Agr	Percent cover of agricultural land	L, U, D	%	30m	2011	CCAP[3]
FormPlan	Percent cover of former plantation land (sugarcane or pineapple)	L, U, D	%	30m	1989	Hawaiʻi OP[3]
Golf	Percent cover of golf course	L, U, D	%	.	1993	Hawaiʻi OP[3]
Mine	Density of quarries	L, U, D	#/km^2	.	2003	USGS MRP[4]
Dam	Density of dams	L, U, D	#/km^2	.	2010	ACOE[5]
RoadLen	Density of roads	L, U, D	km/km^2	1:100,000	2014	TIGER Census[1]
RoadX	Density of road-stream crossings	L, U, D	#/km^2	1:100,000	2014	TIGER Census[1]
DitchLen	Density of agricultural ditches	L, U, D	m/km^2	1:24,000	2004	Hawaiʻi DAR[6]
DitchX	Density of agricultural ditch-stream intersections	L, U, D	#/km^2	1:24,000	2004	Hawaiʻi DAR[6]
PipeLen	Density of utility pipeline length	L, U, D	m/km^2	1:24,000	1983	Hawaiʻi OP[3]
CERCLIS	Density of sites from the Comprehensive Environmental Response, Compensation, and Liability Information System (CERCLIS)	L, U, D	#/km^2	.	2014	EPA[7]
ICIS	Density of sites from the Integrated Compliance Information System (ICIS) and Permit Compliance System (PCS)	L, U, D	#/km^2	.	2014	EPA[7]
TRI	Density of sites from the Toxic Release Inventory (TRI)	L, U, D	#/km^2	.	2014	EPA[7]
UIC	Density of underground injection wells	L, U, D	#/km^2	.	2010	Hawaiʻi DOH[8]
303D	Percent of upstream river network classified as 303D stream with measured TMDL	U	%	1:24,000	2012	EPA[7]

(1) TIGER Census, United States Census Bureau, https://www.census.gov/geo/maps-data/data/tiger.html.
(2) Costal Change Analysis Program, NOAA, https://coast.noaa.gov/digitalcoast/tools/lca.
(3) State of Hawaiʻi Office of Planning, http://planning.hawaii.gov/.
(4) USGS Mineral Resource Program, https://minerals.usgs.gov/.
(5) United States Army Corps of Engineers, http://www.usace.army.mil/.
(6) State of Hawaiʻi Division of Aquatic Resources, dlnr.hawaii.gov/dar/.
(7) United States Environmental Protection Agency, https://www.epa.gov/.
(8) State of Hawaiʻi Department of Health, http://health.hawaii.gov/.

Table 3.5. Highly correlated landscape factors, determined by a Kendall rank correlation test (correlation coefficient ≥ 0.7) on the presence-absence dataset. Landscape factors which were included in the forward selection CCA are indicated with (*).

Retained Factor	**Correlated Factors**				
D_Pop*	D_ImpSur	D_OpDev			
L_DistInl*	D_Area				
L_EsWet*	U_EsWet				
L_FrAqBed*	U_FrAqBed	D_FrAqBed			
L_MeanTemp*	L_MaxTemp	L_MinTemp	L_MpEle	L_MaxEle	
L_MinEle*	L_MpEle	L_MaxEle			
L_RanSoilPerm*	L_StdSoilPerm				
U_Area*	U_SumAnnRain				
U_CERCLIS*	L_CERCLIS	D_CERCLIS			
U_FormPlan*	L_FormPlan				
U_Golf*	L_Golf				
U_ICIS*	L_ICIS				
U_MeanAnnRain*	U_MeanDryRain	U_MeanWetRain	L_MeanDryRain	L_MeanWetRain	L_MeanAnnRain
U_MeanTemp*	U_MaxTemp	U_MinTemp			
U_Pop*	L_Pop				
U_RanAnnRain*	U_StdAnnRain				
U_RoadLen*	U_RoadX				

Table 3.6. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of local population density (L_Pop) on selected taxa using taxon presence-absence by reach to identify threshold for waterfall assessment. (*) indicates the lowest environmental change point that was both positive and significant (i.e., exhibited both a 0.95 purity and 0.95 reliability level) that was selected for the waterfall assessment. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

	zenv. cp	**freq**	**Max grp**	**IndVal**	**obsiv. prob**	**Z score**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z.median**	**filter**
GS	4.24*	87	2	16.47	0.004	11.18	1.43	2.11	4.24	61.07	88.59	0.998	1	11.15	2
GU	5.63	77	2	18.71	0.004	14.83	4.12	4.24	5.54	84.37	190.18	1	1	15.84	2
CM	121.50	11	2	6.89	0.004	7.93	18.11	20.51	122.25	316.09	2291.98	0.978	0.996	9.84	2
CL	64.50	4	2	2.48	0.004	6.06	0.03	0.03	79.82	218.04	335.77	0.854	0.854	6.91	0
WM	4.90	65	2	13.94	0.004	11.71	3.56	3.87	18.80	79.00	114.52	1	1	12.49	2
TI	265.81	27	2	37.96	0.004	25.25	38.19	44.32	519.31	730.38	1003.99	1	1	26.67	2
CC	64.50	7	2	5.13	0.004	9.22	22.36	44.28	77.99	3019.00	3479.62	0.996	0.986	10.51	2
LB	14.76	4	2	1.29	0.076	2.09	0.00	0.00	10.22	134.72	162.06	0.522	0.696	4.61	0
SB	0.00	4	1	3.14	0.032	4.81	0.00	0.00	0.00	153.61	177.25	0.754	0.774	6.39	0
PL	0.03	7	1	1.63	0.252	0.73	0.01	0.02	0.70	16.77	121.13	0.534	0.48	2.46	0
BC	87.66	4	2	2.98	0.004	7.26	14.76	16.48	83.56	213.00	248.50	0.986	0.904	7.27	0
AB	23.37	26	2	5.71	0.004	4.51	0.03	0.03	22.64	1606.99	2481.87	0.804	0.968	6.22	0
TP	0.00	246	1	46.59	0.104	2.19	0.00	0.00	91.12	643.99	1014.11	0.756	0.892	3.26	0
RS	960.26	20	2	10.16	0.076	3.02	0.00	0.00	422.19	1762.59	1935.82	0.716	0.822	4.98	0

Table 3.7. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of local road length density (L_RoadLen) on selected taxa using taxon presence-absence by reach to identify threshold for waterfall assessment. (*) indicates the lowest environmental change point that was both positive and significant (i.e., exhibited both a 0.95 purity and 0.95 reliability level) that was selected for the waterfall assessment. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

	zenv. cp	**freq**	**Max grp**	**IndVal**	**obsiv.prob**	**Z score**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z.median**	**filter**
GS	0.85	87	2	10.60	0.004	3.55	0.00	0.00	0.74	6.04	6.49	0.826	0.926	4.10	0
GU	0.49	77	2	15.17	0.004	11.43	0.00	0.00	0.40	0.66	0.84	1	1	10.89	2
CM	1.09	11	2	3.18	0.004	4.82	0.74	0.86	13.11	20.67	21.14	0.974	0.946	6.59	0
CL	0.44	4	2	1.24	0.084	2.43	0.13	0.34	0.53	2.80	4.10	0.958	0.578	2.85	0
WM	0.01*	65	2	11.76	0.004	7.65	0.00	0.00	1.67	4.62	5.24	0.998	1	9.33	2
TI	7.39	27	2	25.87	0.004	18.44	1.69	3.96	7.90	9.51	10.19	1	1	20.15	2
CC	0.00	7	2	2.03	0.012	3.89	0.01	0.09	2.74	12.86	13.19	0.996	0.9	4.87	0
LB	3.24	4	2	1.38	0.068	2.46	0.35	0.48	2.60	3.50	5.25	0.972	0.604	3.51	0
SB	0.47	4	2	1.24	0.06	2.23	0.01	0.26	1.43	3.99	4.22	0.96	0.632	3.21	0
PL	0.00	7	2	1.46	0.148	1.23	0.00	0.00	0.06	5.09	5.17	0.452	0.432	2.34	0
BC	0.00	4	2	0.92	0.26	1.05	0.00	0.00	0.87	2.60	4.21	0.546	0.298	2.10	0
AB	6.99	26	2	7.77	0.024	3.43	0.00	0.30	5.33	10.63	11.97	0.918	0.88	5.07	0
TP	0.00	246	1	49.69	0.168	1.83	0.00	0.00	3.86	15.37	15.45	0.514	0.896	3.16	0
RS	0.00	20	2	4.03	0.004	3.87	0.00	0.00	0.61	9.17	10.59	0.936	0.9	4.68	0

Table 3.8. Distribution of surveys from the augmented presence-absence dataset that occured upstream of human influences (UHI,as designated by local population density and local road length density thresholds) by island. UHI surveys were grouped by occurrence above various waterfall height classes (0.0-5.0 m, 5.1-10.0 m, 10.1-20.0 m, 20.1-30.0 m, and > 30.0 m).

Island	**Total Surveys**	**Surveys UHI**	**Number of UHI surveys upstream of waterfalls height (m)**				
			0.0-5.0	**5.1-10.0**	**10.1-20.0**	**20.1-30.0**	> **30.0**
Kaua'i	1662	345	29	1	0	34	0
O'ahu	2049	408	0	0	0	0	0
Moloka'i	904	612	113	13	67	0	0
Maui	1999	662	98	49	41	48	4
Hawai'i	2539	141	16	0	41	0	0

Table 3.9. Distribution of surveys from the augmented presence-absence dataset that occured upstream of human influences (UHI,as designated by local population density and local road length density thresholds) by taxa. UHI surveys were grouped by occurrence above various waterfall height classes (0.0-5.0 m, 5.1-10.0 m, 10.1-20.0 m, 20.1-30.0 m, and > 30.0 m). GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, and RS = Red Swamp Crayfish.

Taxa	Total Surveys	Surveys UHI	Number of UHI surveys upstream of waterfalls height (m)				
			0.0-5.0	5.1-10.0	10.1-20.0	20.1-30.0	> 30.0
TP	1527	390	27	0	3	4	0
AB	43	7	0	0	3	0	0
GS	544	48	0	0	0	0	0
PL	22	7	0	0	0	0	0
WM	143	6	0	0	0	0	0
SB	28	4	0	0	0	0	0
RS	118	2	0	0	0	0	0
LB	11	1	0	0	0	0	0
GU	310	0	-	-	-	-	-
CM	62	0	-	-	-	-	-
CL	5	0	-	-	-	-	-
TI	57	0	-	-	-	-	-
CC	12	0	-	-	-	-	-
BC	30	0	-	-	-	-	-

Table 3.10. Forward selection canonical correspondence analysis results of selected taxa composition with significant ($p \leq 0.01$) landscape environmental factors using taxon presence-absence at the reach-scale (591 reaches, 13 taxa, 24 degrees of freedom). (*) indicated the factors that were kept among all the correlated landscape factors.

Summary:

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4478	0.2454	0.2026	0.157
Explained variation (cumulative)	8.420	13.04	16.85	19.81
Pseudo-canonical correlation	0.8059	0.6368	0.5589	0.6376
Explained fitted variation (cumulative)	32.12	49.73	64.26	75.52

Forward Selection Results:

Name	Explains %	Contribution %	pseudo-F	P
D_Slope	4.4	8.6	15	0.002
U_MeanAnnRain*	2.7	5.3	9.4	0.002
L_OpWater	2.0	3.8	7.0	0.002
D_OpWater	1.6	3.1	5.8	0.002
D_ICIS	1.5	2.9	5.5	0.002
U_MaxAnnRain	1.2	2.3	4.5	0.002
U_Pop*	1.1	2.2	4.2	0.01
U_PipeLen	1.2	2.3	4.4	0.002
D_DitchLen	1.0	2.0	4.0	0.002
U_MeanTemp*	1.0	1.9	3.8	0.002
D_MaxSl	0.9	1.8	3.6	0.002
U_CERCLIS*	1.1	2.1	4.2	0.01
U_MinSoilPerm	0.9	1.7	3.5	0.002
U_RoadLen*	0.8	1.6	3.2	0.002
U_RanAnnRain*	0.7	1.4	3.0	0.004
U_Shrub	0.7	1.4	2.9	0.002
D_DitchX	0.7	1.4	2.9	0.004
U_MaxSoilPerm	0.6	1.2	2.4	0.008
D_FormPlan	0.7	1.3	2.7	0.01
D_Shrub	0.6	1.2	2.4	0.006
L_PipeLen	0.6	1.2	2.6	0.008

Table 3.11. Summary of TITAN environmental changing-points for selected taxa using reach presence-absence . Nine out of 14 taxa exhibited significant response to the selected 13 natural and nine anthropogenic landscape factors (refer to Table 3.2 and 3.4 for the definition of the landscape factors). Positive changing-point values indicated that taxa presence increased at the changing-point, whereas negative values indicated taxa presence decreased at the changing-point. The taxa Cuban Limia (CL), Largemouth Bass (LB), Smallmouth Bass (SB), Pond Loach (PL), and Bristle-nosed Catfish (BC) did not exhibit changing-points that met purity and reliability criteria (0.95 and 0.95 respectively). Furthermore, no significant changing-points were found fot the landscape factors upstream pipeline length (U_PipeLen), local pipeline length (L_PipeLen), upstream CERCLIS sites (U_CERCLIS), or downstream former plantation (D_FormPlan). GS = Green Swordtail, GU = Guppy, CM = Common Molly, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, AB= American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Natural Factors	**GS**	**GU**	**CM**	**WM**	**TI**	**CC**	**AB**	**TP**	**RS**
D_Slope	-4.06	-3.64	-2.51	-4.45	-0.57	-2.06			
D_MaxSl	-9.87	-9.72	-3.45	-9.87	-0.86	-3.30		-12.78	
U_MeanAnnRain	-5000.34		-3393.25	-2373.48	-2789.85			2472.56	
U_MaxAnnRain		8920.75		-3886.34	-1603.25			2858.53	-2542.87
L_MinEle	-209.00	-229.00	-28.00	-209.00	-3.00			-80.00	
U_MeanTemp	20.62	20.62	21.61	22.95	23.65	21.90			
L_OpenWater	-0.00	-0.06		-0.00	0.10			-4.39	-0.03
D_OpenWater	-1.14	-0.41			2.30				
U_MaxSoilPerm	-4.00	-4.39		-4.00		-4.00			
U_MinSoilPerm	-3.60		-0.70		-0.70	-0.70	-0.92		
U_RanAnnRain	614.93	465.19		-994.28	-695.01				
U_Shrub	9.78	9.70	51.97				9.27		
D_Shrub		5.39							
Anthropogenic Factors	**GS**	**GU**	**CM**	**WM**	**TI**	**CC**	**AB**	**TP**	**RS**
U_Pop	3.76	4.17	25.68	23.14	131.09	40.86			516.61
U_RoadLen		7.08	0.21	1.67	2.26		0.41	-2.29	6.73
D_ICIS	0.23	1.05		0.47	0.12			-0.00	
D_DitchLen	699.31	1636.30		1811.68					228.82
D_DitchX		0.12							

Chapter Three Figures

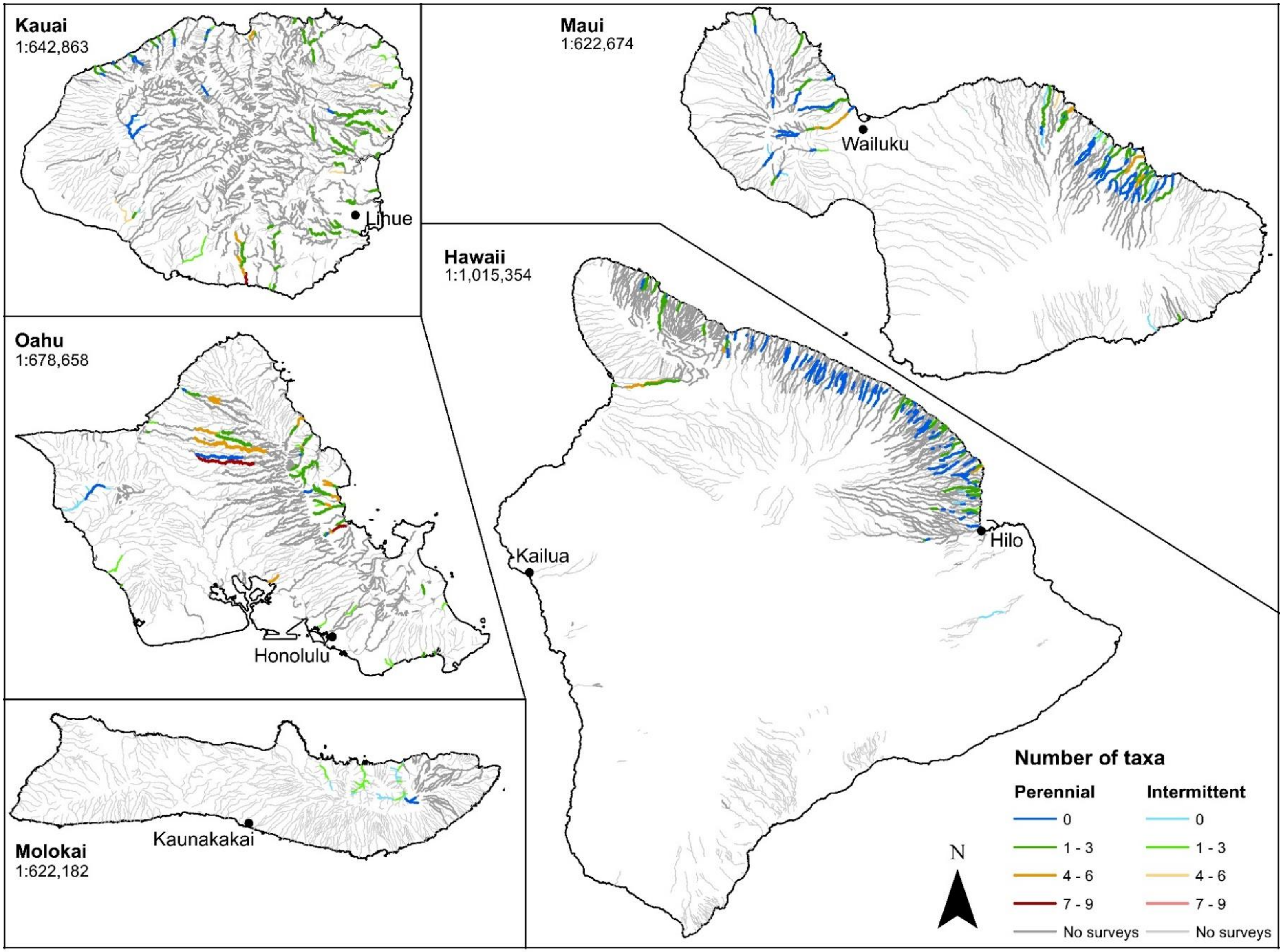


Figure 3.1. Spatial distribution of number of introduced taxa occurrences by reach.

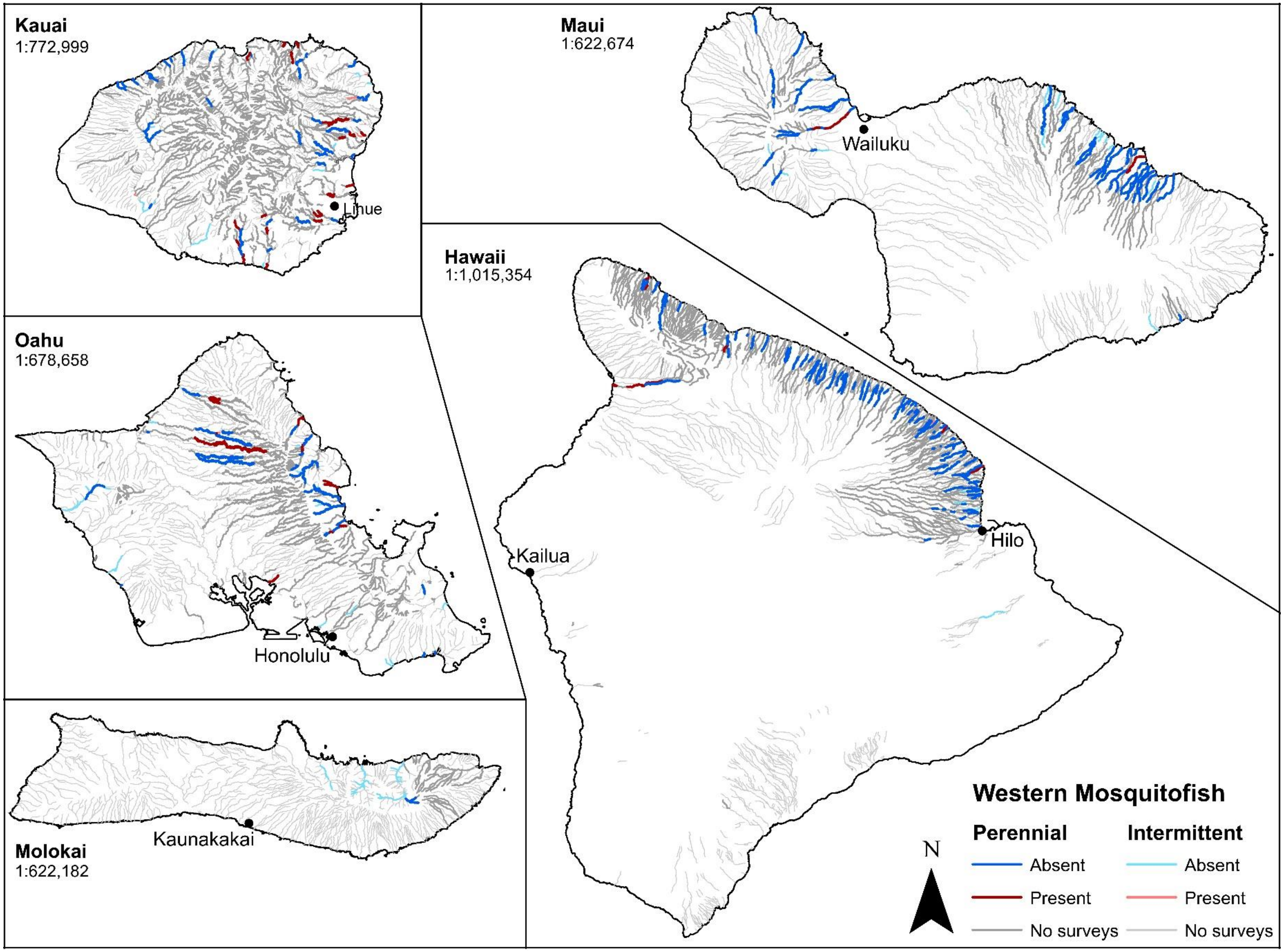


Figure 3.2. Spatial distribution of Western Mosquitofish occurrences by reach.

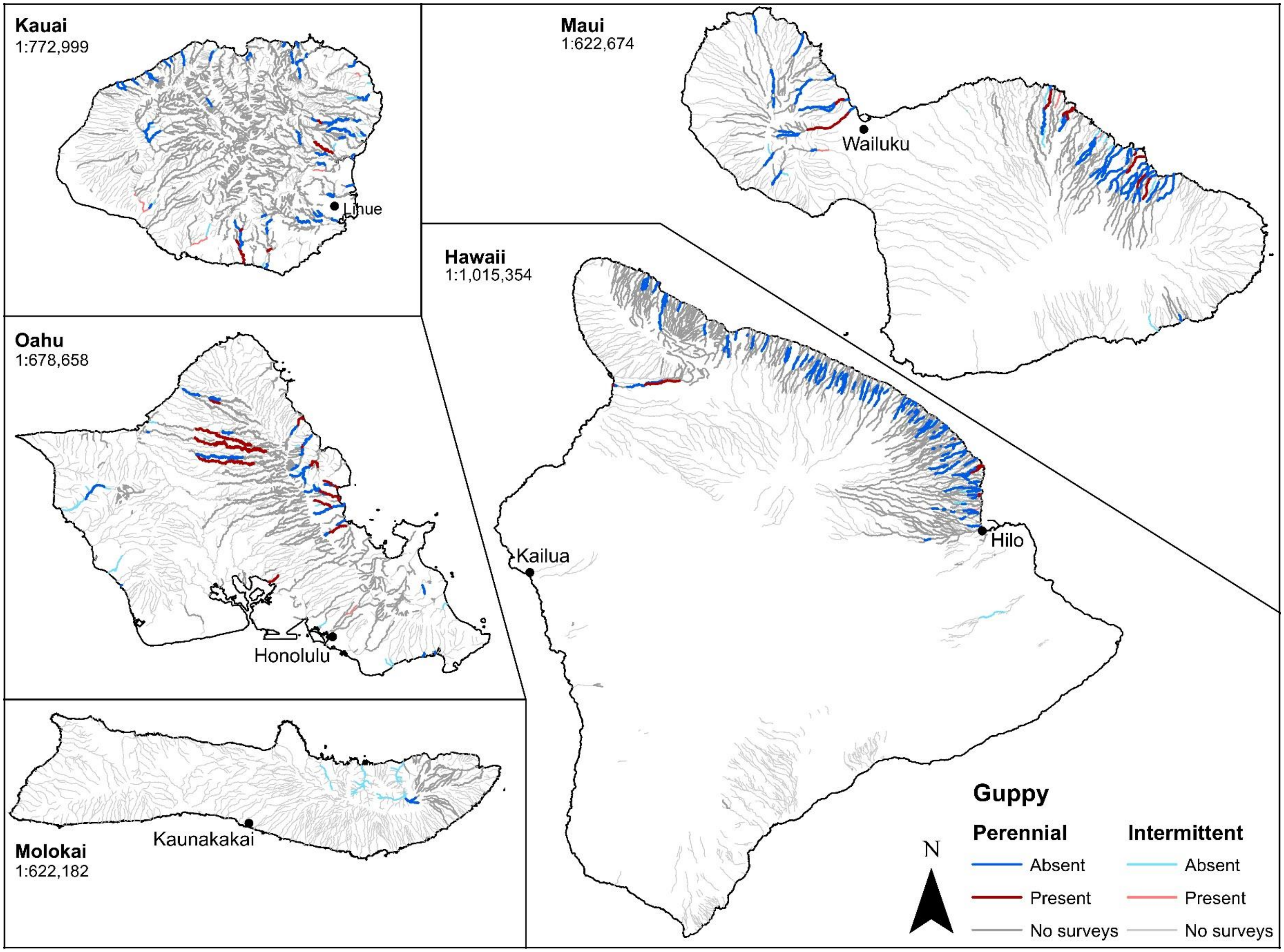


Figure 3.3. Spatial distribution of Guppy occurrences by reach.

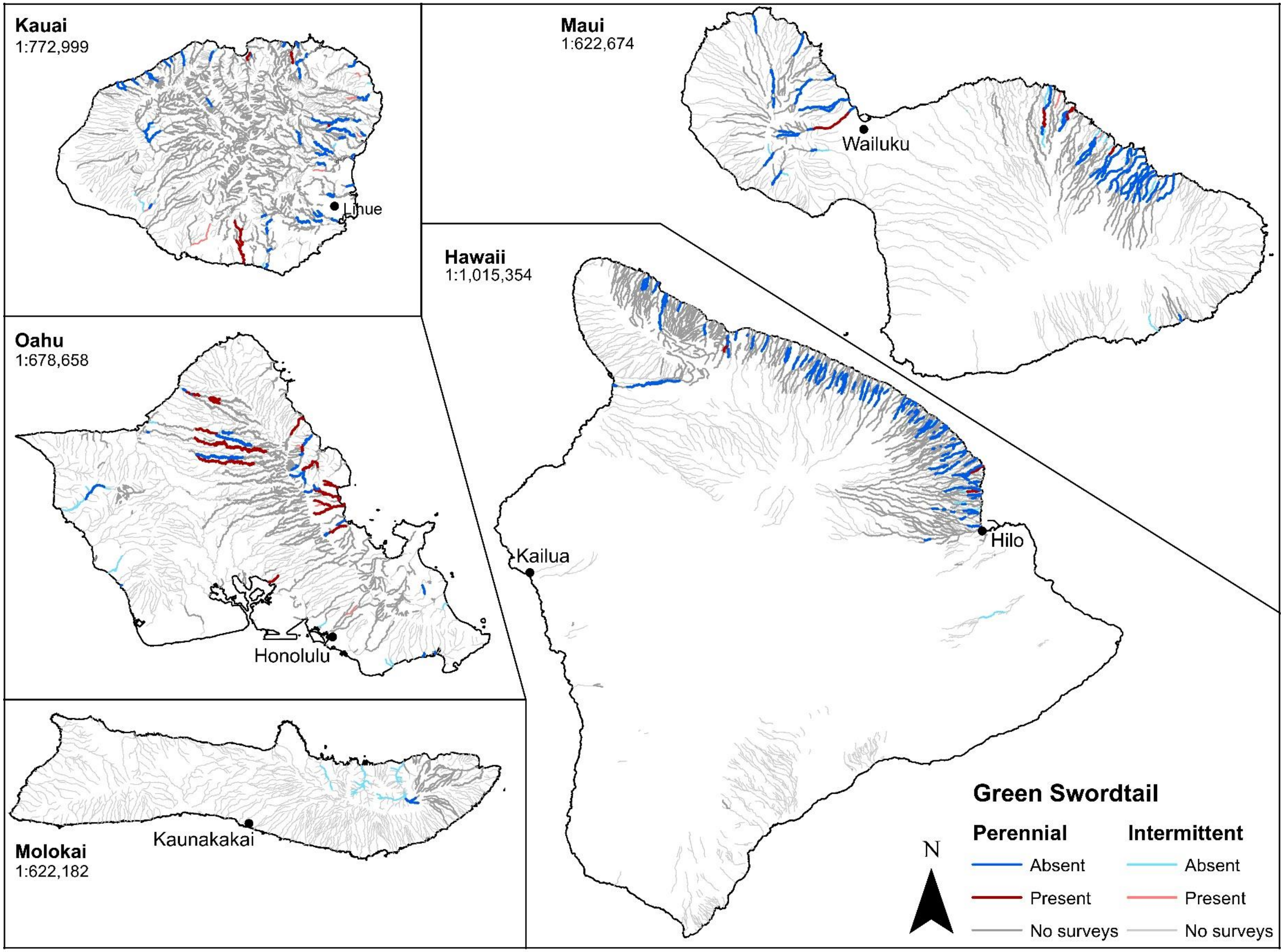


Figure 3.4. Spatial distribution of Green Swordtail occurrences by reach.

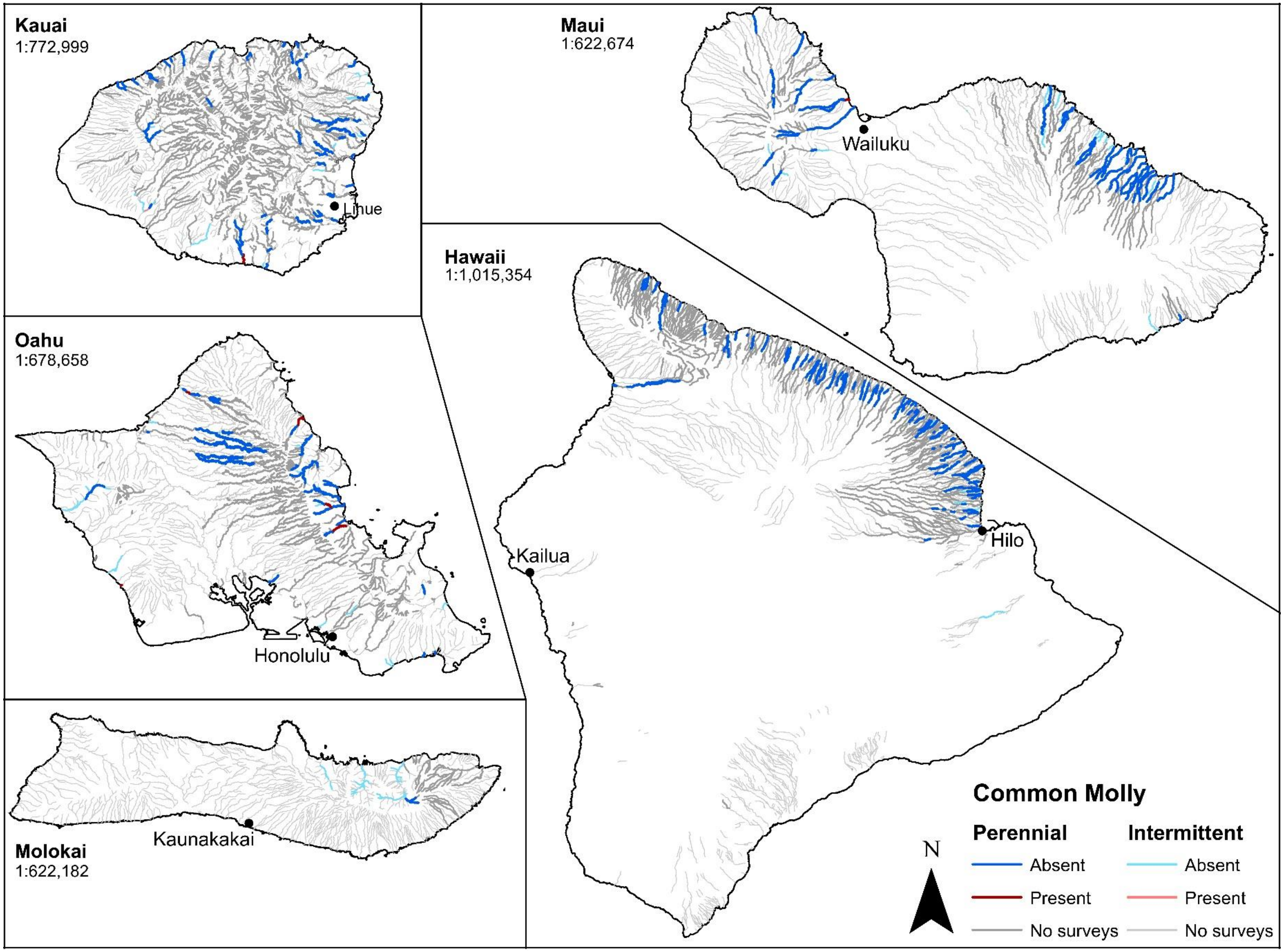


Figure 3.5. Spatial distribution of Common Molly occurrences by reach.

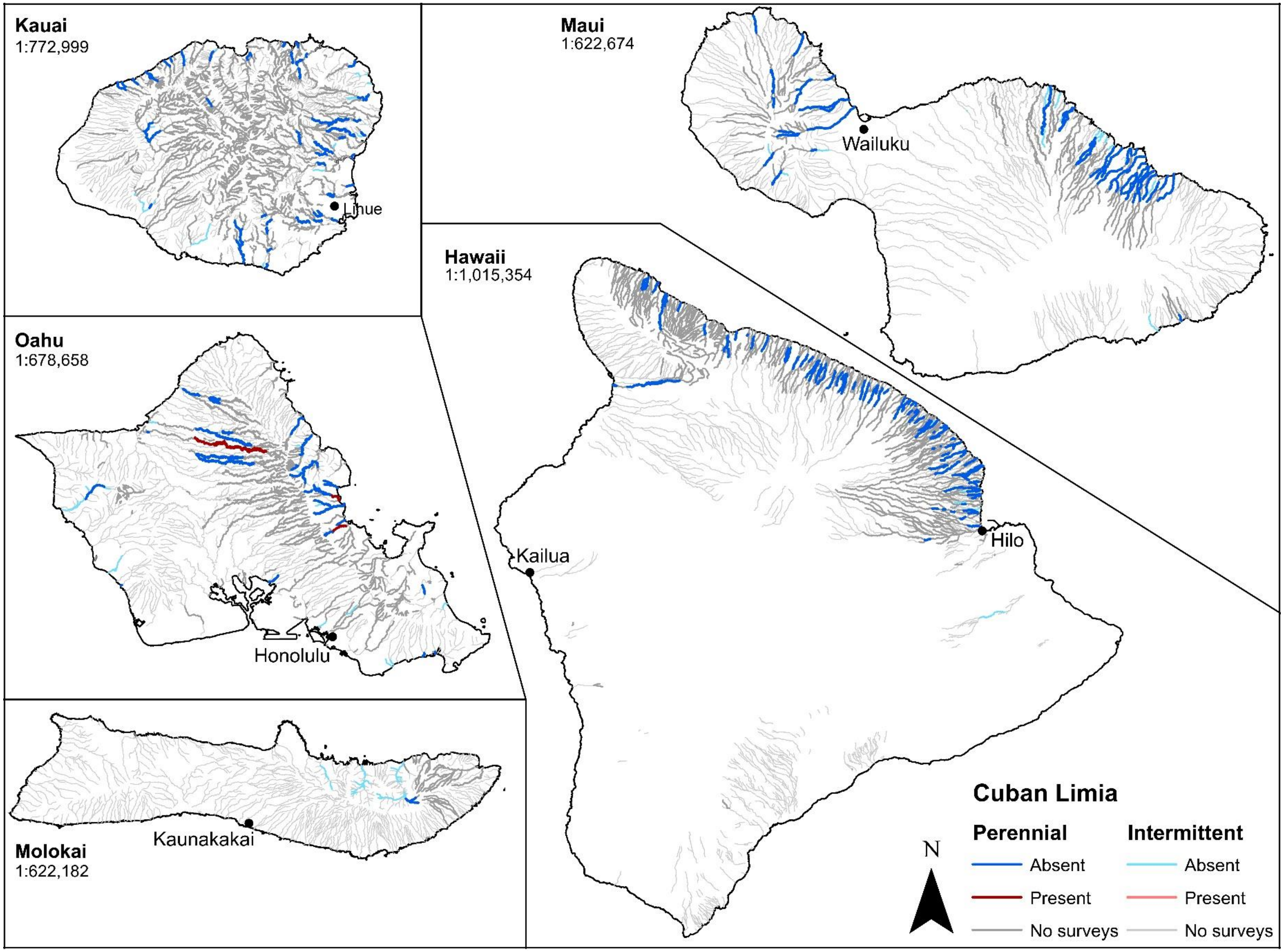


Figure 3.6. Spatial distribution of Cuban Limia occurrences by reach.

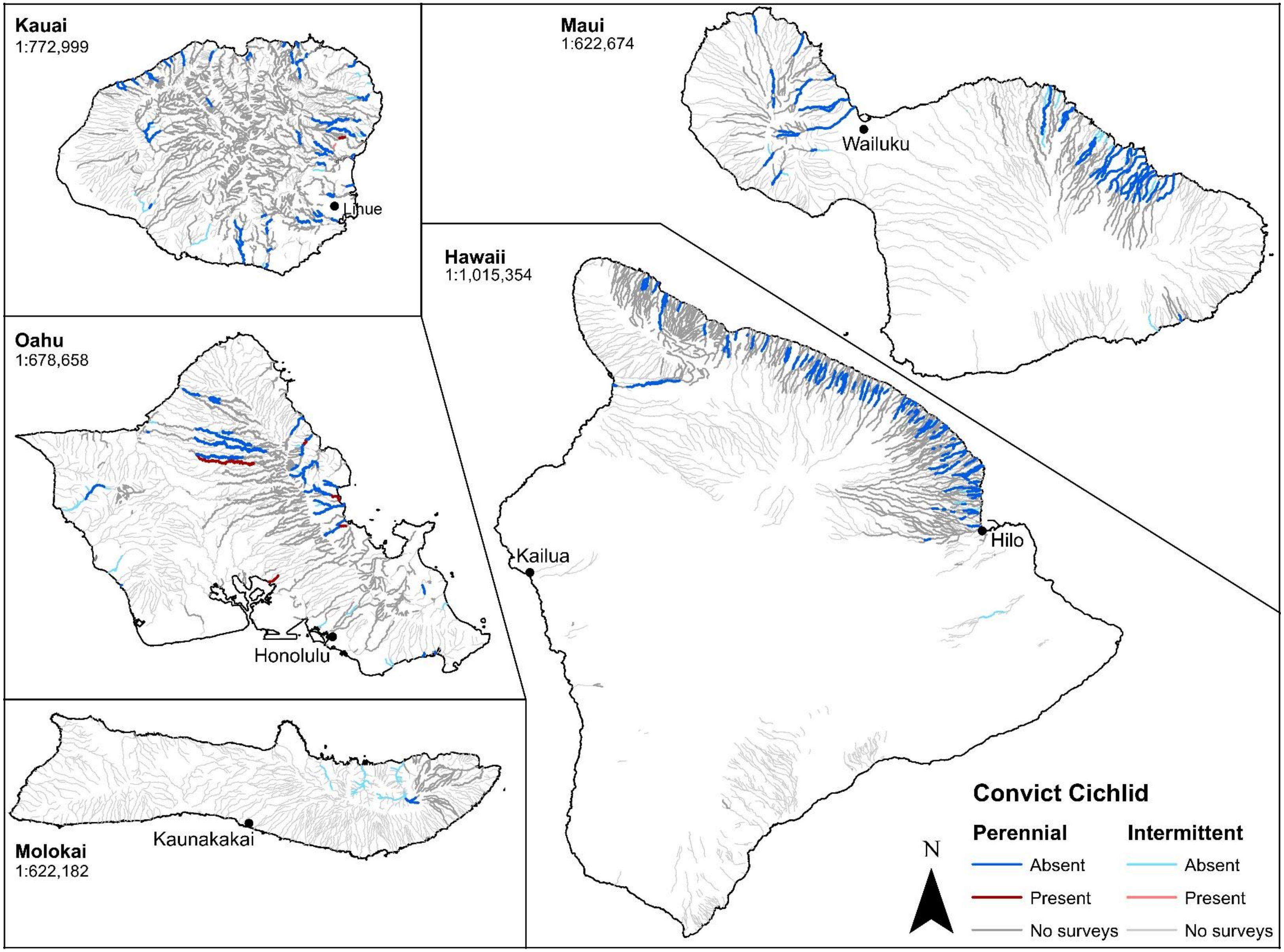


Figure 3.7. Spatial distribution of Convict Cichlid occurrences by reach.

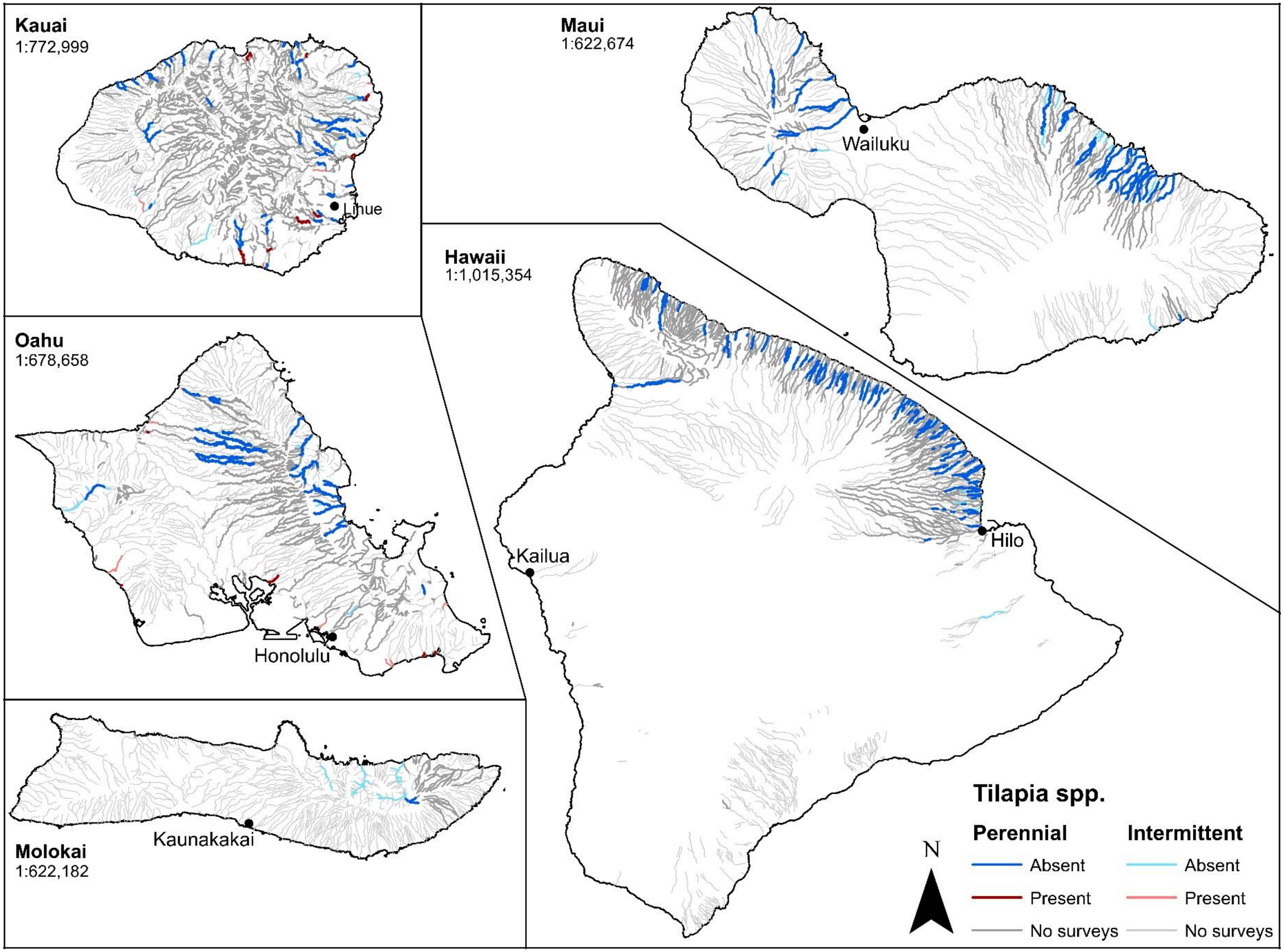


Figure 3.8. Spatial distribution of tilapia occurrences by reach.

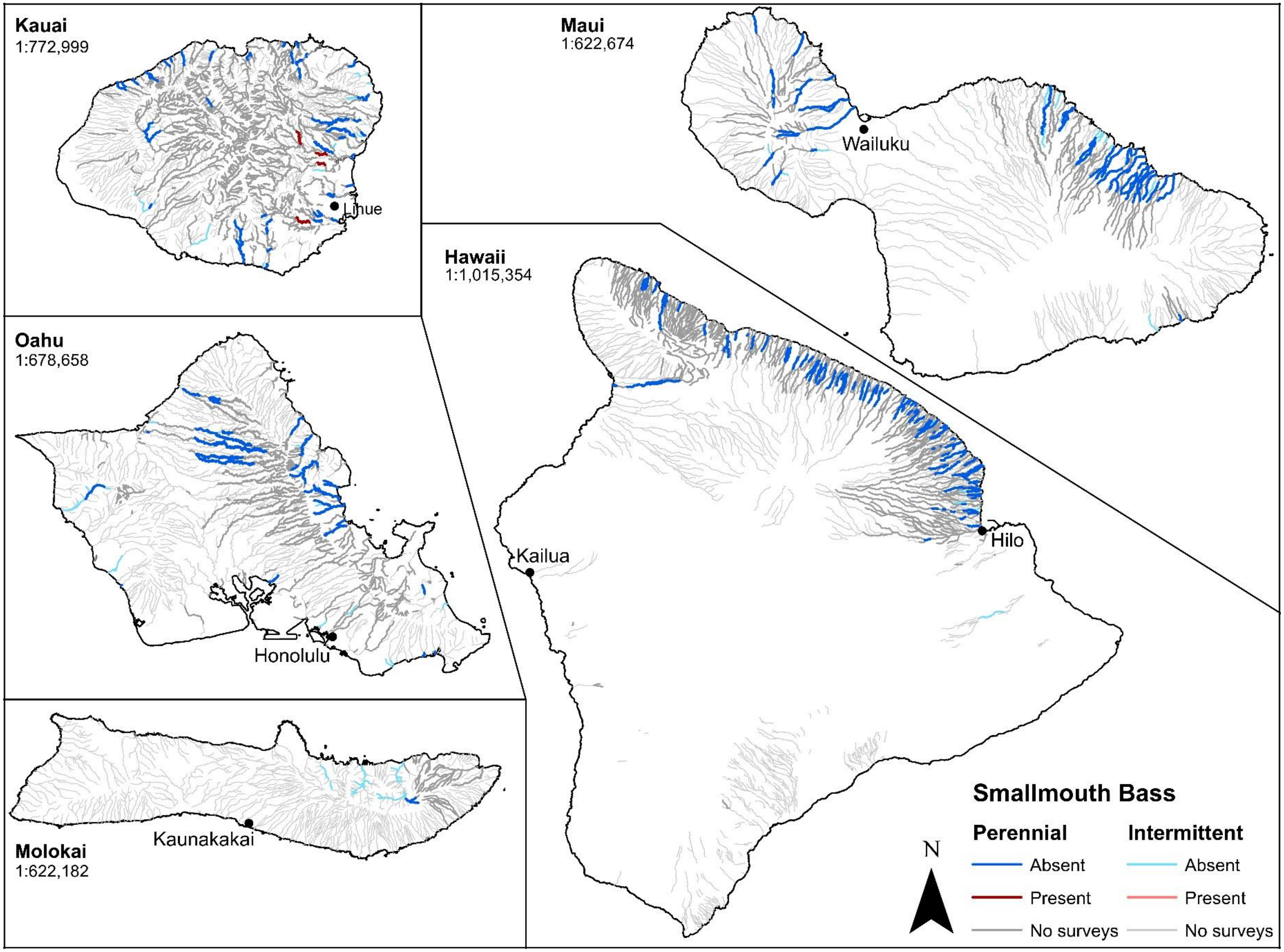


Figure 3.9. Spatial distribution of Smallmouth Bass occurrences by reach.

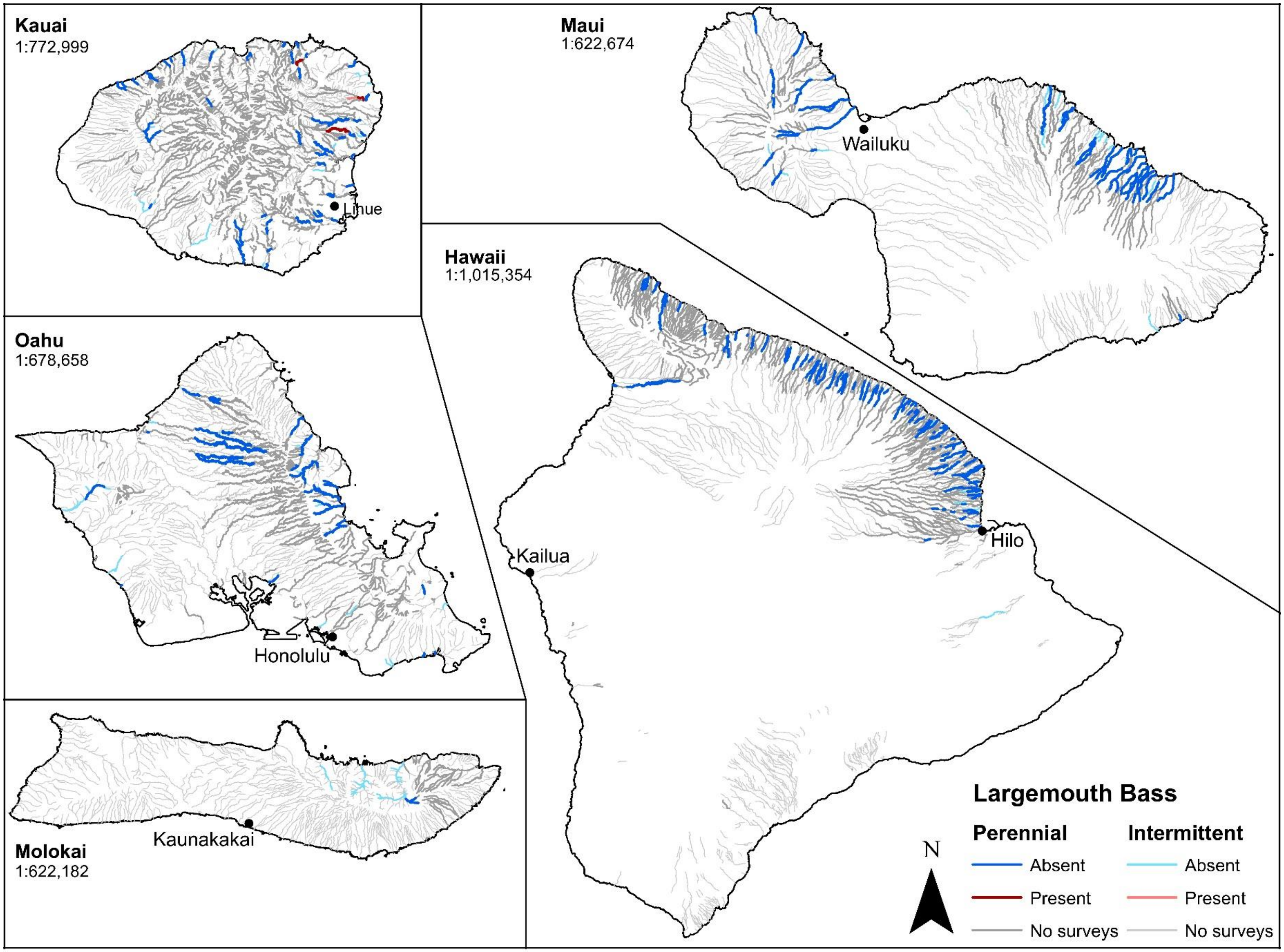


Figure 3.10. Spatial distribution of Largemouth Bass occurrences by reach.

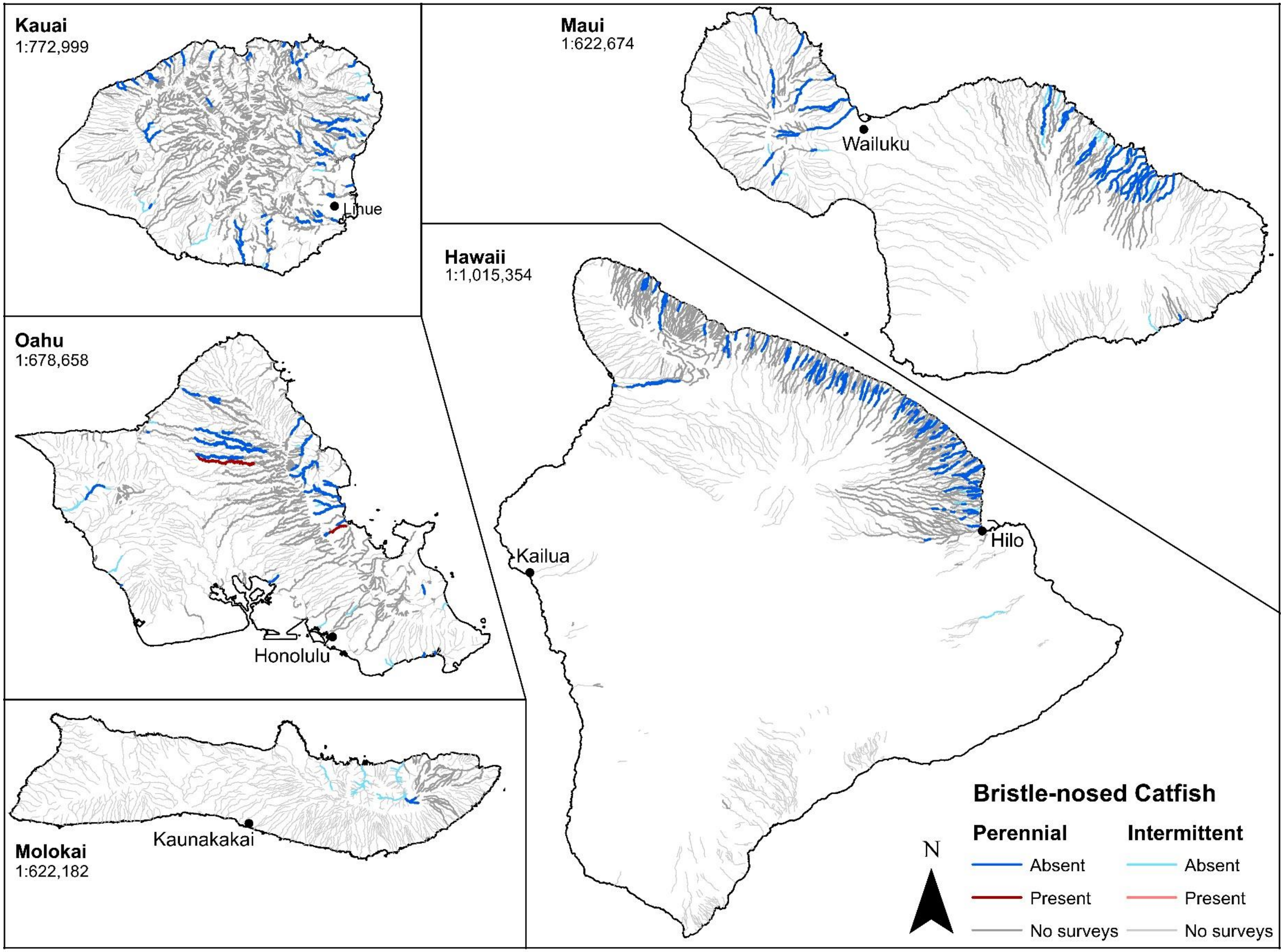


Figure 3.11. Spatial distribution of Bristle-nosed Catfish occurrences by reach.

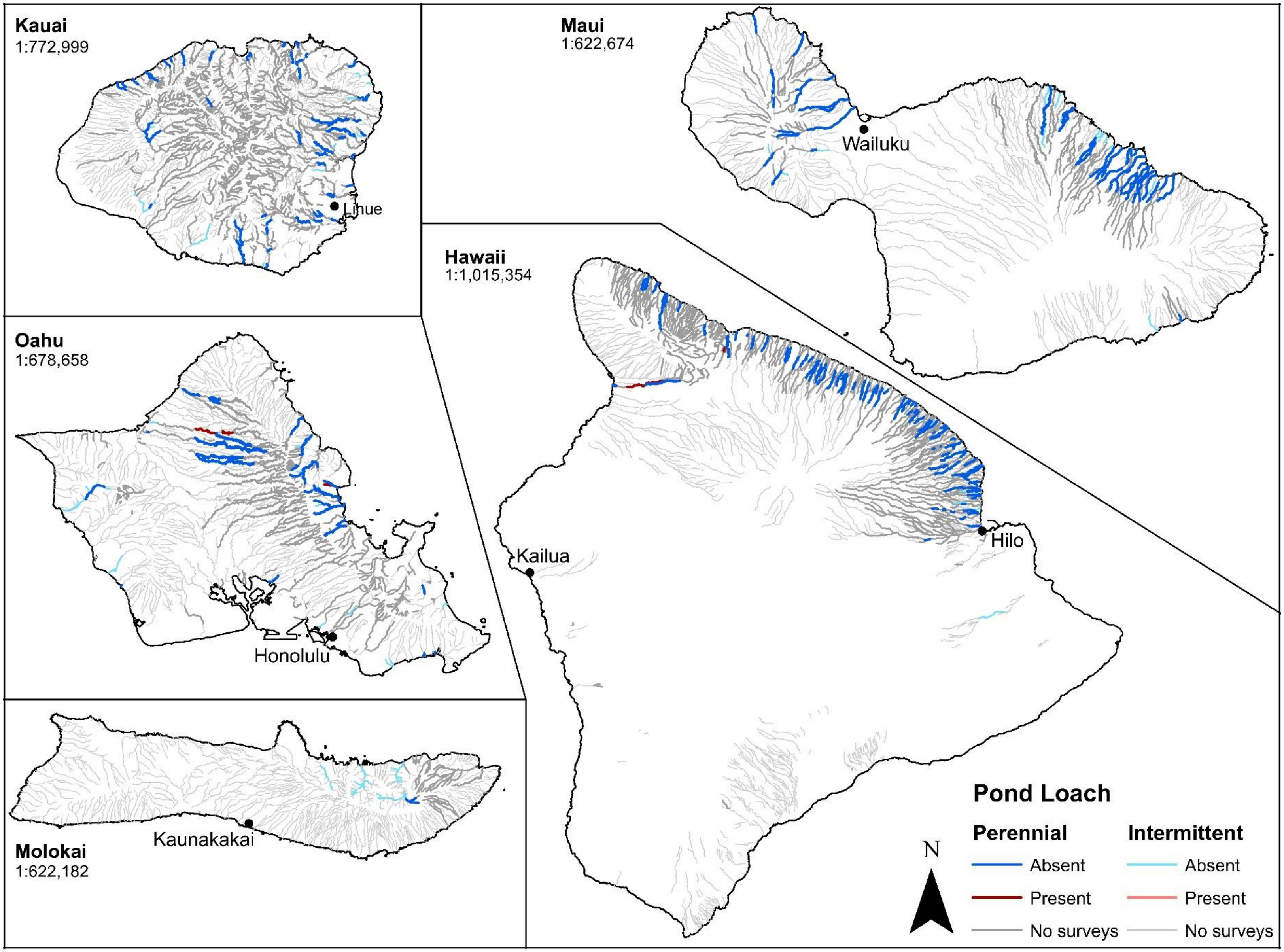


Figure 3.12. Spatial distribution of Pond Loach occurrences by reach.

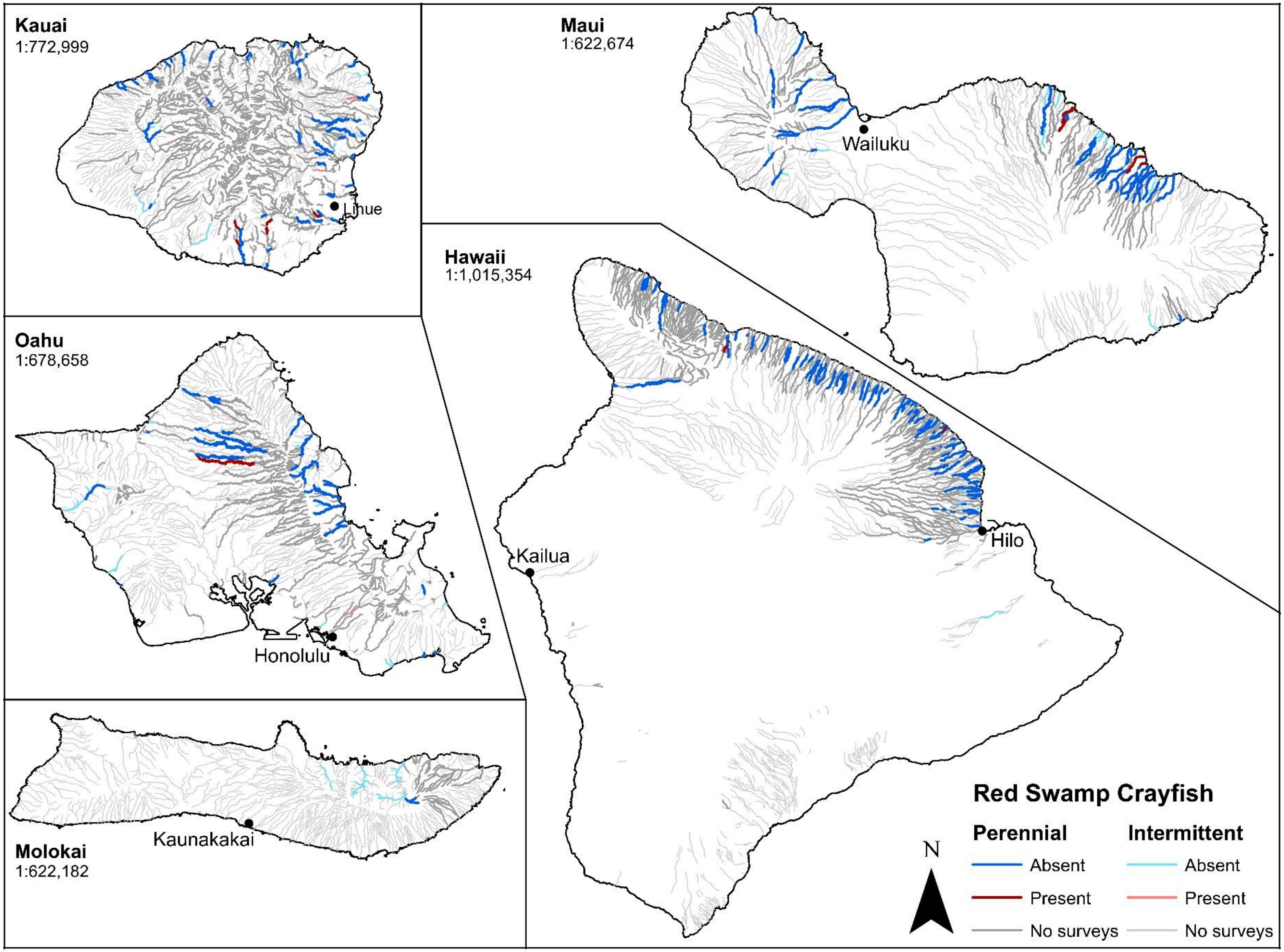


Figure 3.13. Spatial distribution of Red Swamp Crayfish occurrences by reach.

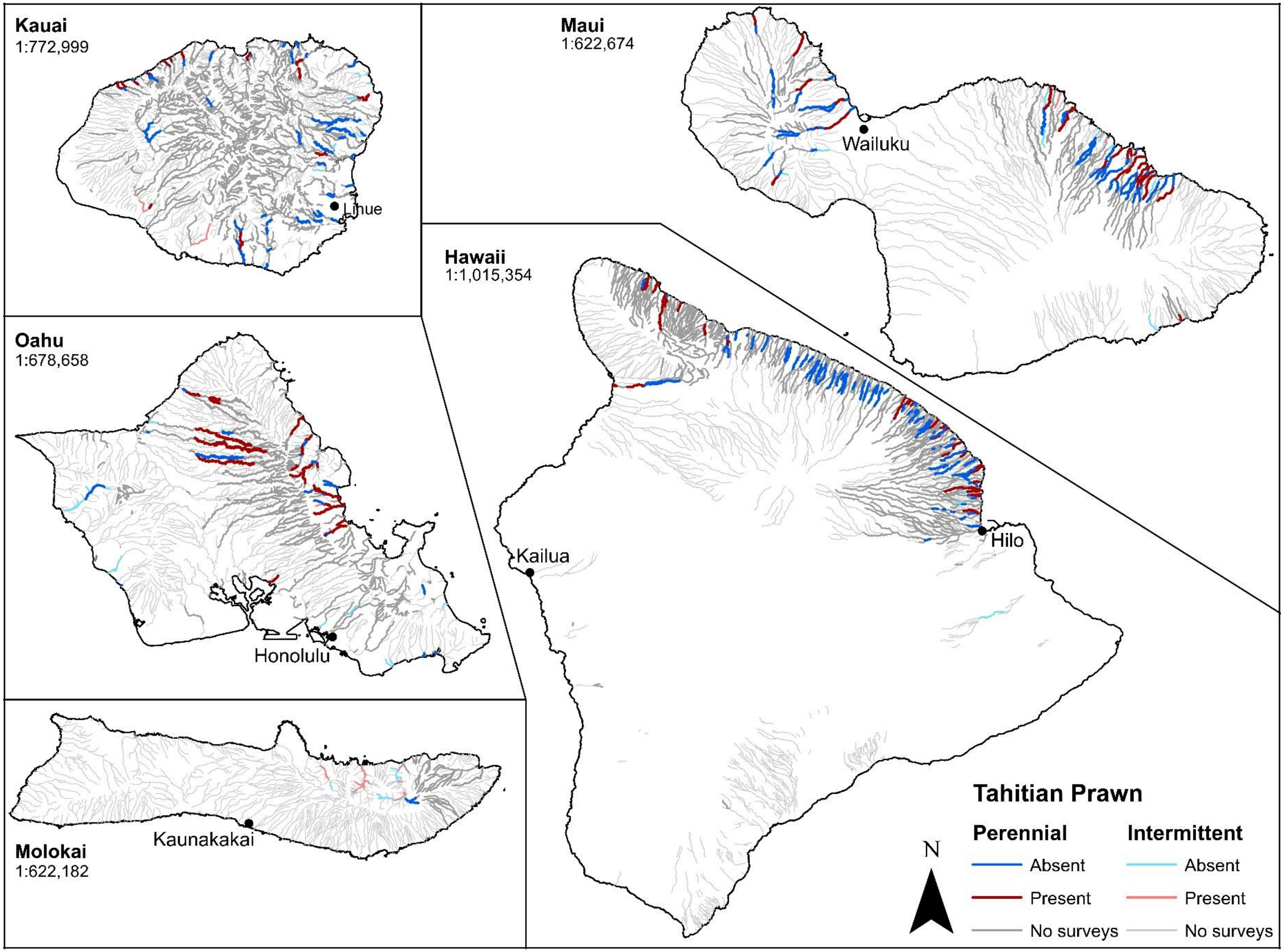


Figure 3.14. Spatial distribution of Tahitian Prawn occurrences by reach.

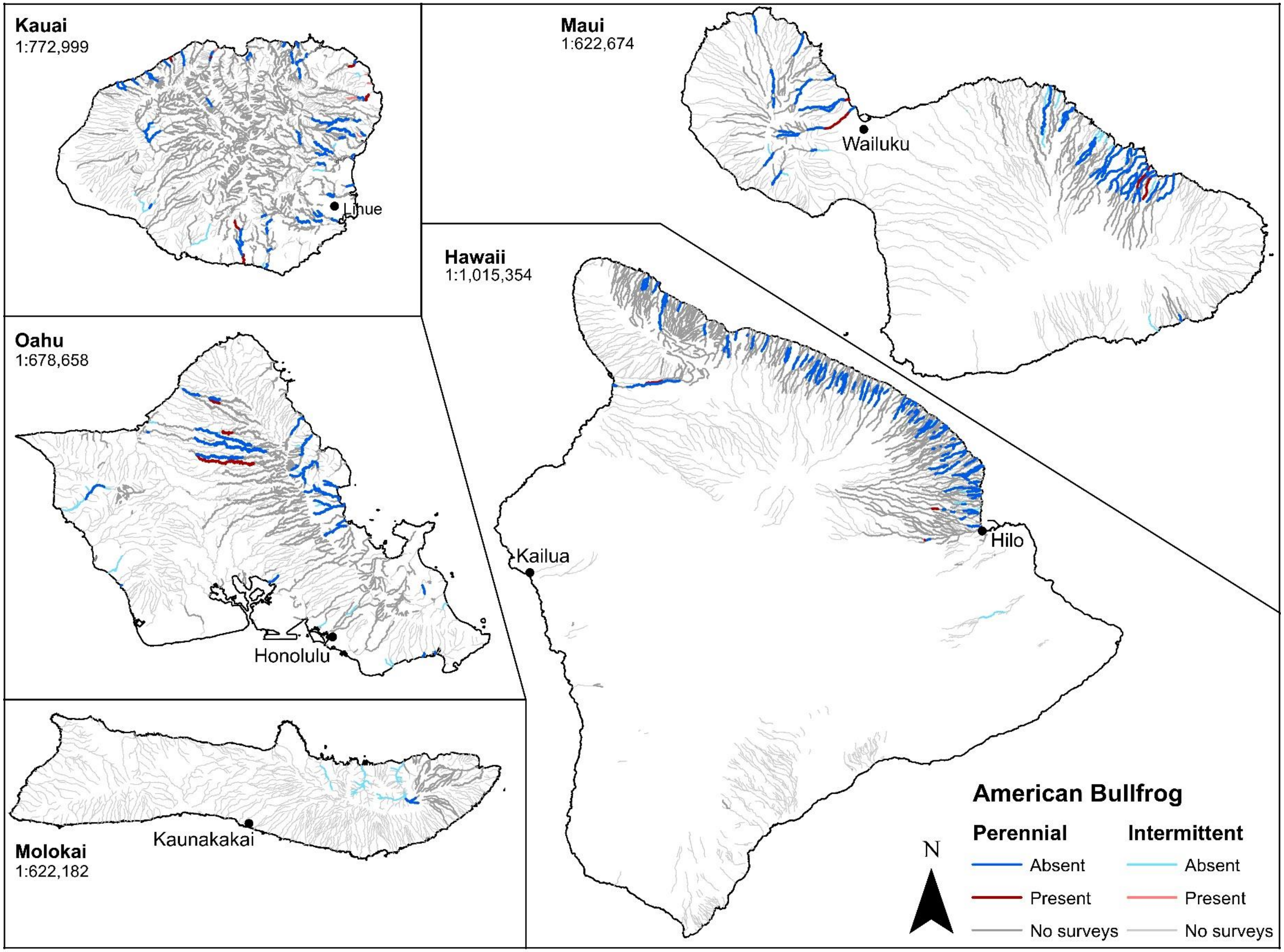


Figure 3.15. Spatial distribution of American Bullfrog occurrences by reach.

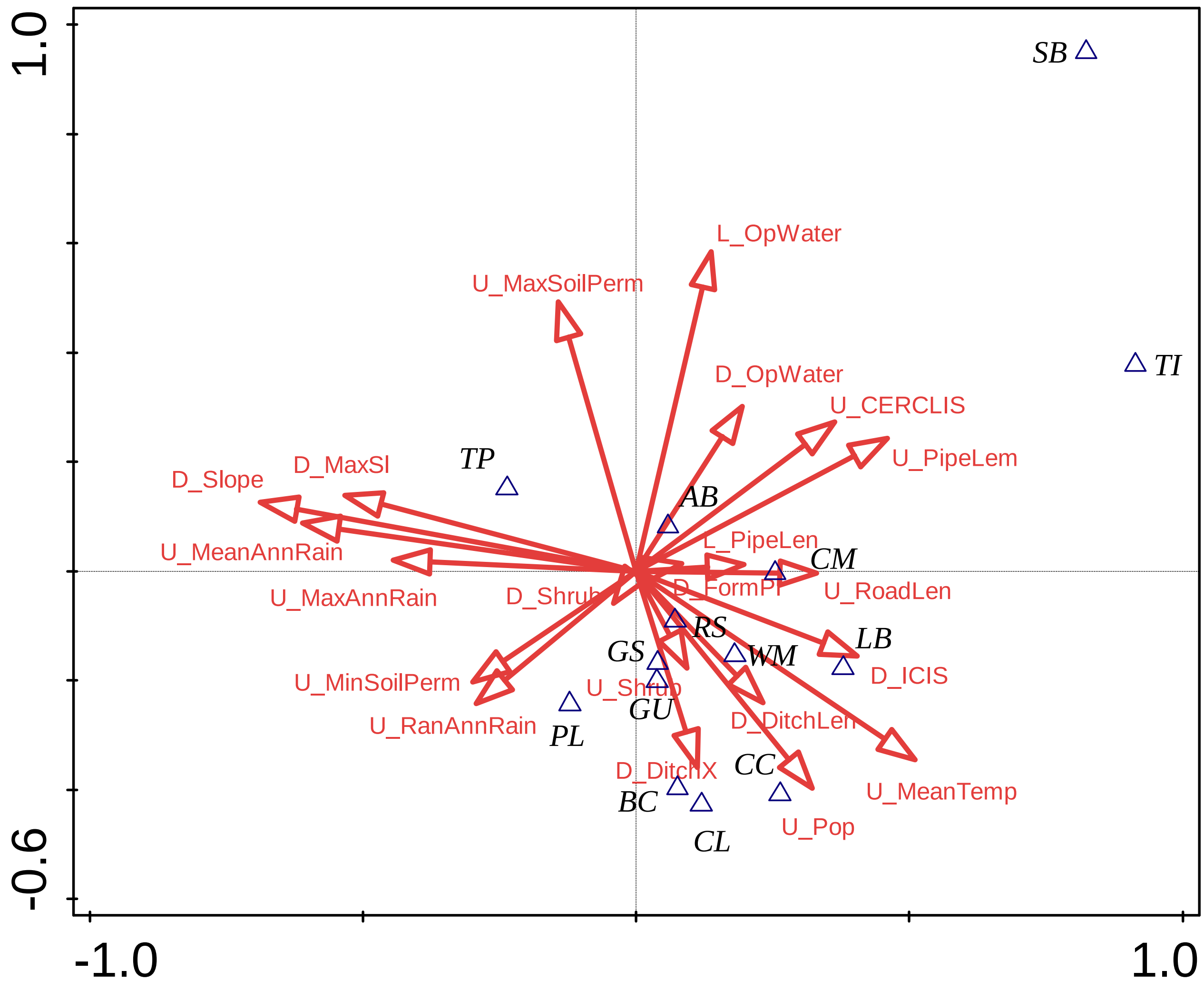
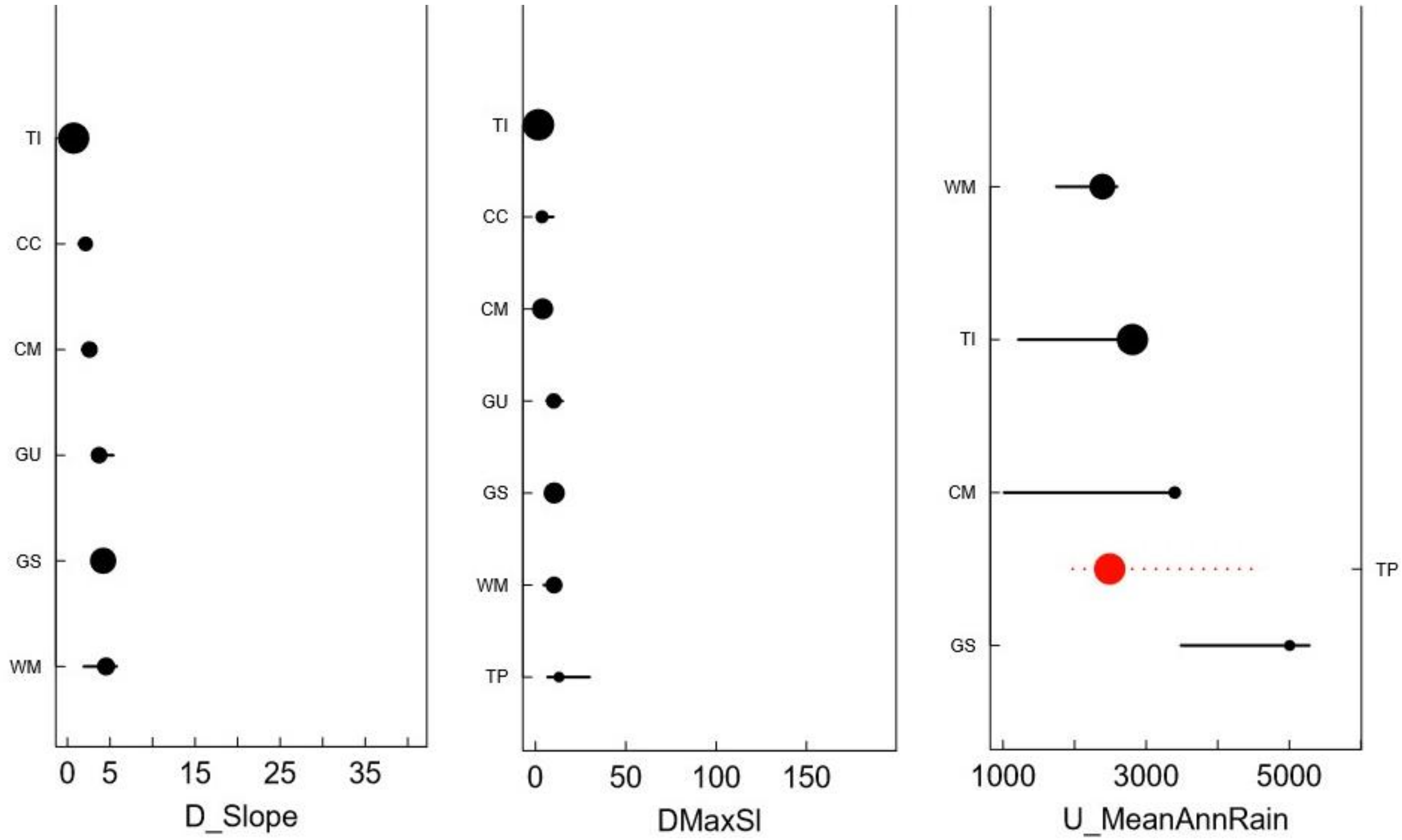
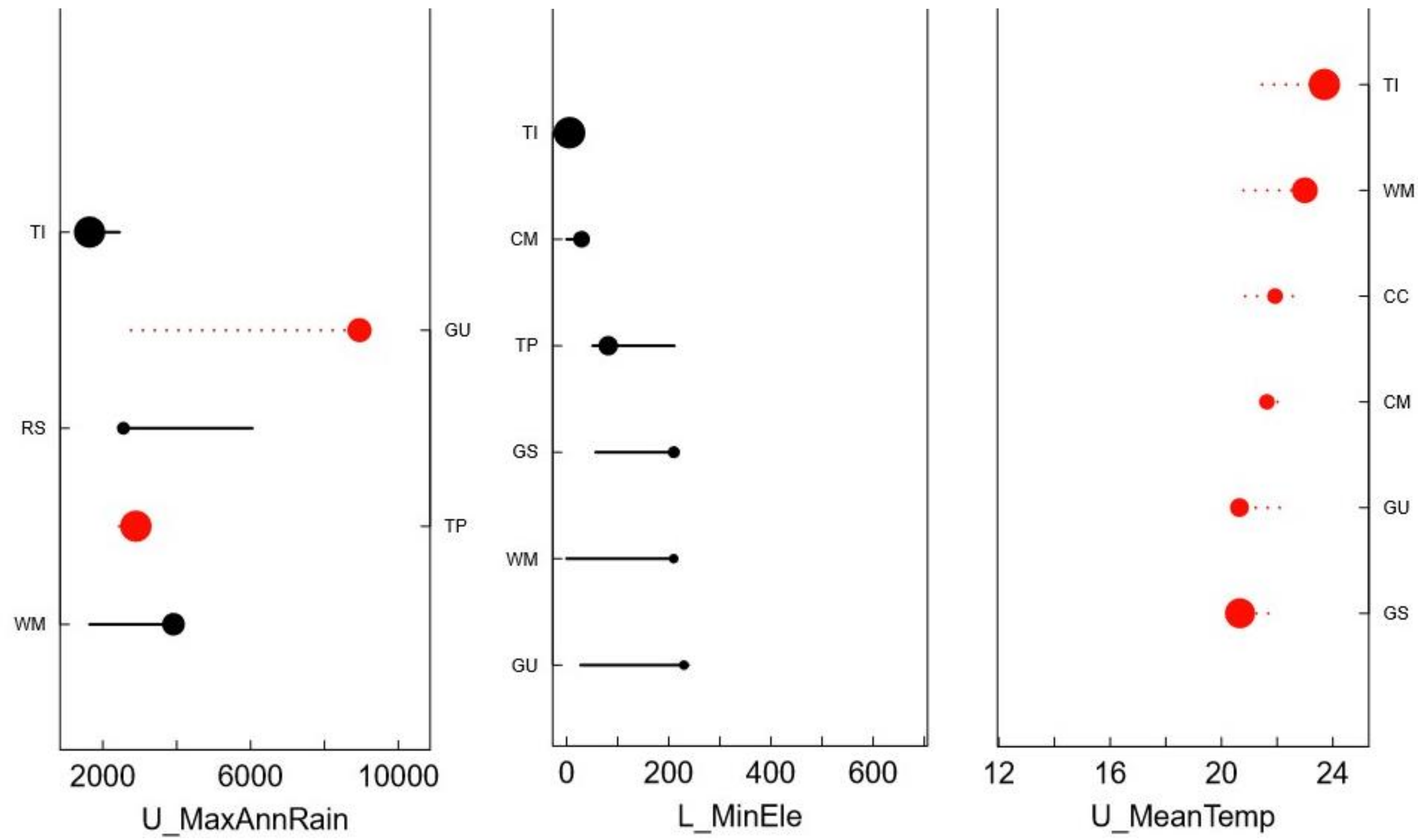


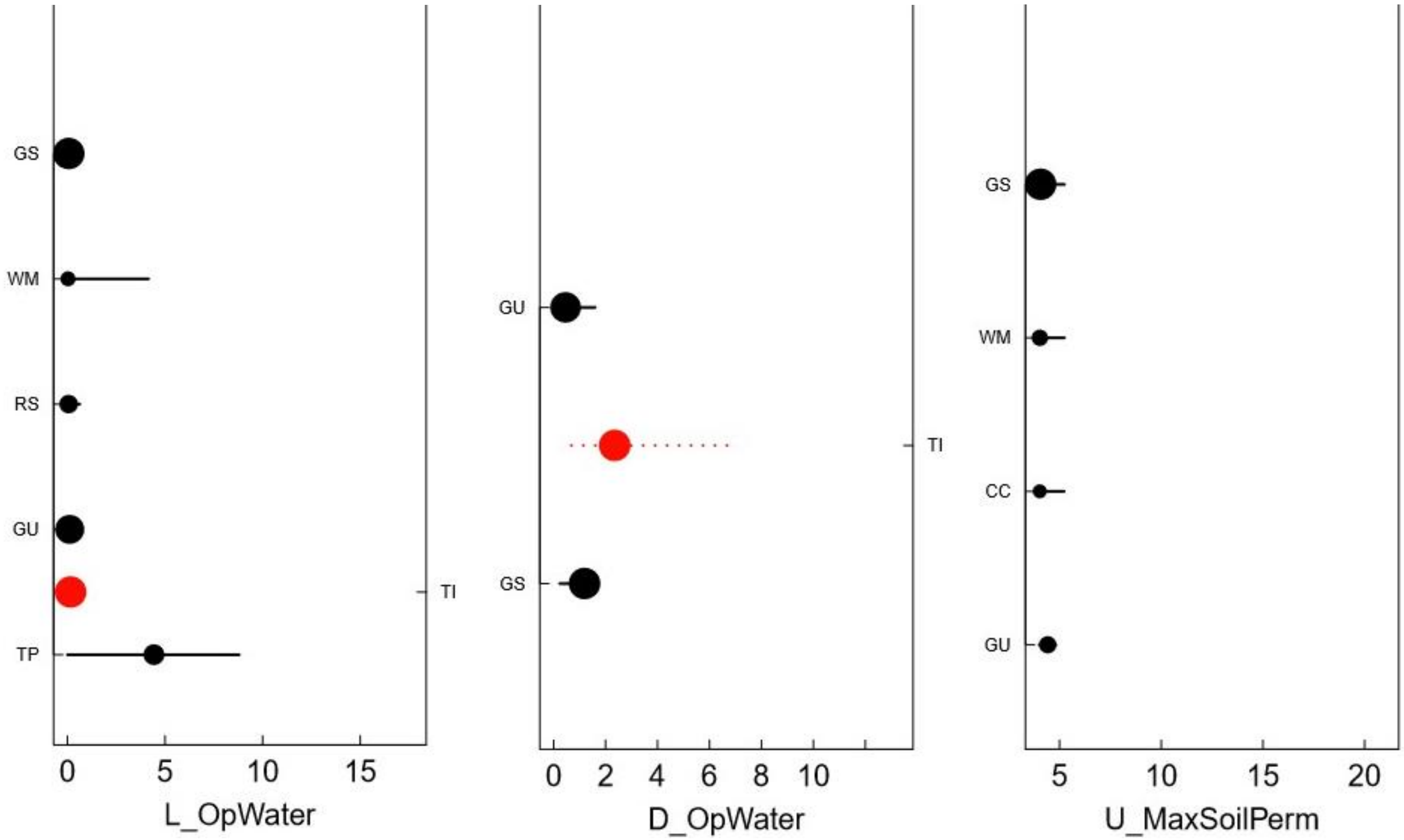
Figure 3.16. Forward selection Canonical Correspondence Analysis biplot of selected taxa composition with significant (P ≤ 0.01) landscape factors using taxon presence-absence dataset at the reach scale (591 reaches, 349 reaches with selected taxa, 14 taxa, 24 degrees of freedom). Landscape factor abbreviations are listed in Table 3.3 and 3.4, taxa codes are GS = Green Swordtail, CM = Common Molly, CL = Cuban Lima, GU = Guppy, WM = Western Mosquitofish, CC = Convict Cichlid, TI = tilapia, BC = Bristle-nosed Catfish, SB = Smallmouth Bass, LB = Largemouth Bass, PL = Pond Loach, TP = Tahitian Prawn, RS = Red Swamp Crayfish, AB = American Bullfrog.



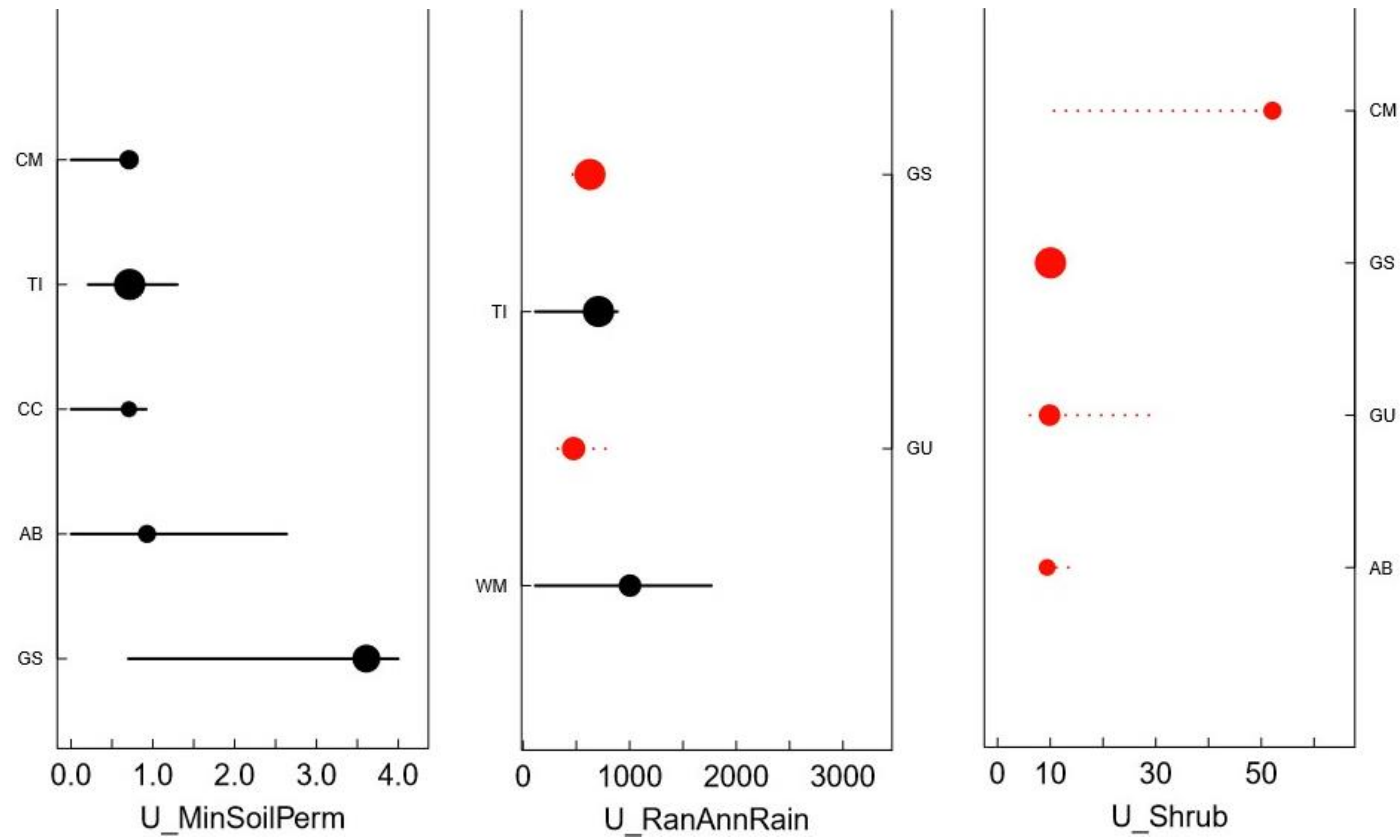
Figures 3.17 – 3.19. TITAN results using taxon presence-absence at the reach-scale, for the landscape factors downstream channel slope (D_Slope; Figure 3.17), downstream maximum channel slope (DMaxSl; Figure 3.18) and upstream mean annual rainfall (U_MeanAnnRain; Figure 3.19). Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental changing-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish, TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.



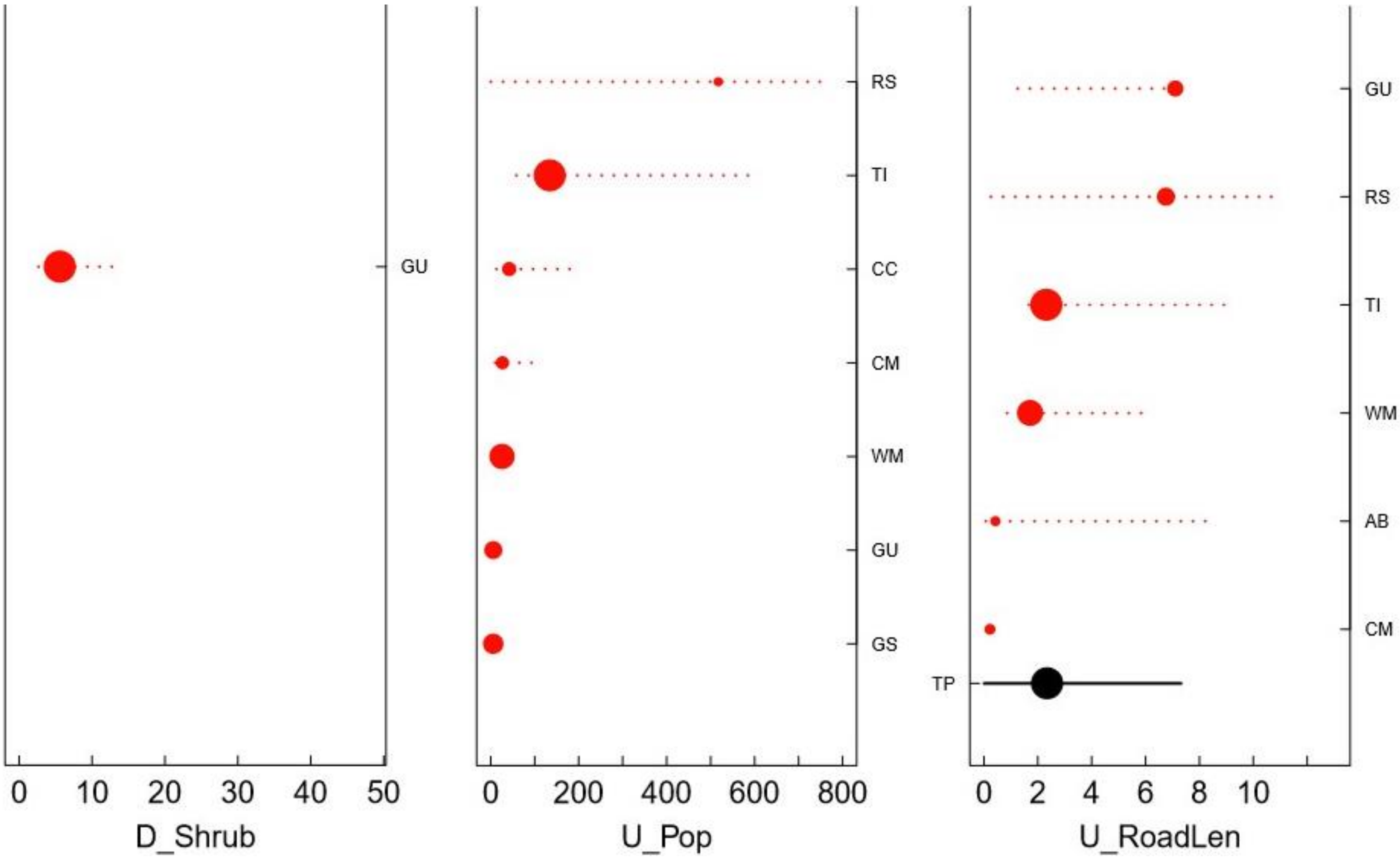
Figures 3.20 – 3.22. TITAN results using taxon presence-absence at the reach-scale, for the landscape factors upstream maximum annual rinfall (U_MaxAnnRain; Figure 3.20), local minimum reach elevation (L_MinEle; Figure 3.21) upstream mean air temperature (U_MeanTemp; Figure 3.22). Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental changing-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish, TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.



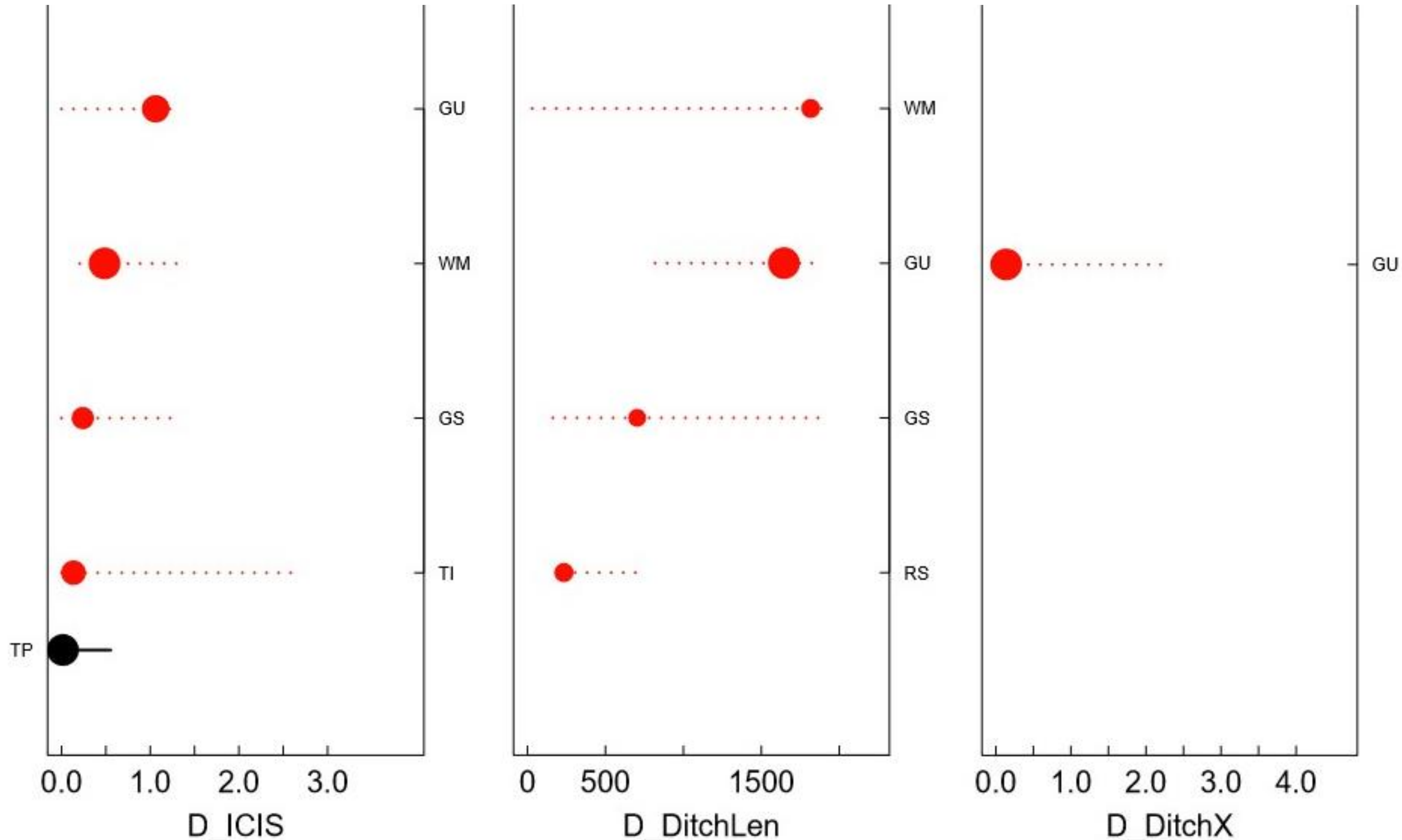
Figures 3.23 – 3.25. TITAN results using taxon presence-absence at the reach-scale, for the landscape factors local percent open water (L_OpWater; Figure 3.23), downstream percent open water (D_OpWater; Figure 3.24), and upstream maximum soil permeability (U_MaxSoilPerm; Figure 3.24). Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental changing-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish, TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.



Figures 3.26 – 3.28. TITAN results using taxon presence-absence at the reach-scale, for the landscape factors upstream minimum soil permeability (U_MinSoilPerm; Figure 3.26), Upstream range of annual rainfall (U_RanAnnRain; Figure 3.27), and upstream shrubland (U_Shrub; Figure 3.28) Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental changing-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish, TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.



Figures 3.29 – 3.31. TITAN results using taxon presence-absence at the reach-scale, for the landscape factors downstream shrubland (D_Shrub; Figure 3.29), upstream population density (U_Pop; Figure 3.30), and upstream road length density (U_RoadLen; Figure 3.31). Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental chaging-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish,TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.



Figures 3.32 – 3.34. TITAN results using taxon presence-absence at the reach-scale, for the landscape factors downstream ICIS site (D_ICIS; Figure 3.32), downstream ditch length (D_DitchLen; Figure 3.33), and downstream ditch intersections (D_DitchX; Figure 3.34). Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental changing-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish, TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.

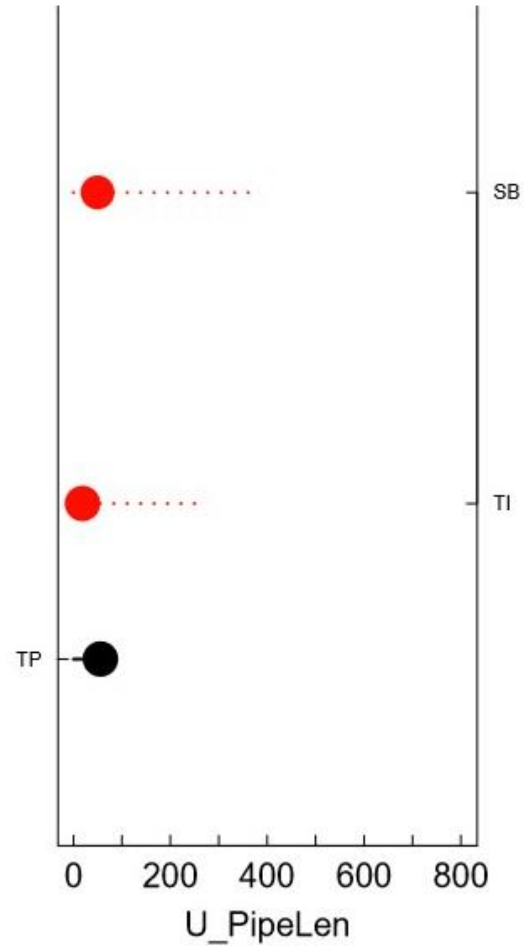


Figure 3.35. TITAN results using taxon presence-absence at the reach-scale, for the landscape factor upstream pipeline length (U_PipeLen). Pure (≥95) and reliable (≥95) indicator taxa are plotted in increasing order with respect to their observed environmental changing-point. Black symbols correspond to negative (z) indicator taxa, whereas red corresponds to positive (z+) indicator taxa. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. Taxa codes are GS = Green Swordtail, CM = Common Molly, GU = Guppy, WM = Western Mosquitofish, TP = Tahitian Prawn, RS = Red Swamp Crayfish, TI = tilapia, AB = American Bullfrog.

Chapter Three Supplemental Tables

Table S 3.1. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream channel slope (D_Slope) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	4.06	87	1	27.72	0.004	21.61	3.51	3.58	3.92	4.54	4.75	1.000	1.000	22.26	1	4.06
GU	3.64	77	1	19.20	0.004	12.75	3.47	3.52	3.66	5.33	5.40	1.000	1.000	13.09	1	3.64
CM	2.51	11	1	7.28	0.004	12.67	1.76	1.82	2.46	2.59	2.71	1.000	1.000	12.50	1	2.51
CL	1.82	4	1	3.54	0.004	8.37	1.39	1.66	1.82	2.06	2.26	0.972	0.908	8.14	0	1.82
WM	4.45	65	1	17.25	0.004	14.09	1.93	2.49	4.71	5.62	5.78	1.000	1.000	14.03	1	4.45
TI	0.57	27	1	68.60	0.004	26.29	0.25	0.31	0.67	1.45	1.55	1.000	1.000	28.10	1	0.57
CC	2.06	7	1	5.47	0.004	11.21	1.31	1.38	1.65	1.89	2.03	1.000	0.996	11.93	1	2.06
LB	2.26	4	1	2.92	0.004	5.99	1.18	1.32	2.27	2.50	2.58	0.976	0.906	6.85	0	2.26
SB	1.57	4	1	3.71	0.008	8.32	1.42	1.51	1.76	2.15	2.27	0.988	0.912	8.38	0	1.57
PL	11.86	7	1	1.42	0.312	0.44	2.01	2.05	5.47	9.48	11.35	0.550	0.372	2.01	0	11.86
BC	1.78	4	1	2.69	0.008	6.20	1.60	1.65	2.38	2.53	2.58	0.984	0.918	7.16	0	1.78
AB	3.20	23	1	6.43	0.004	6.29	1.63	1.66	3.15	13.26	31.53	0.894	0.992	7.24	0	3.20
TP	16.31	232	2	32.69	0.016	3.08	1.82	4.71	14.03	31.01	38.70	0.634	0.986	4.75	0	16.31
RS	4.74	20	1	3.29	0.040	1.88	1.77	1.82	4.72	8.64	11.73	0.762	0.690	2.85	0	4.74

Table S 3.2. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream maximum channel slope (DMaxSl) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	**zenv. cp**	**freq**	**max grp**	**Ind Val**	**obsiv. prob**	**z score**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z. median**	**filter**	**zenv. cp**
GS	9.87	87	1	23.57	0.004	17.08	5.63	5.70	7.30	10.37	11.20	1.000	1.000	17.63	1	9.87
GU	9.72	77	1	18.02	0.004	11.80	6.18	7.28	9.60	14.87	14.99	1.000	1.000	12.39	1	9.72
CM	3.45	11	1	12.97	0.004	17.04	2.53	2.62	3.62	4.29	5.51	1.000	1.000	16.24	1	3.45
CL	3.32	4	1	4.10	0.004	10.68	2.42	2.61	2.97	9.67	9.76	0.988	0.874	8.21	0	3.32
WM	9.87	65	1	17.11	0.004	13.16	4.55	5.34	8.09	10.79	13.79	0.998	1.000	13.78	1	9.87
TI	0.86	27	1	76.86	0.004	26.74	0.63	0.74	1.41	3.33	3.45	1.000	1.000	29.47	1	0.86
CC	3.30	7	1	6.99	0.004	9.57	1.80	2.13	3.32	5.55	9.76	0.998	0.976	10.42	1	3.30
LB	3.33	4	1	3.98	0.004	8.02	1.95	2.14	2.91	3.93	6.58	0.934	0.784	7.68	0	3.33
SB	152.17	4	2	32.83	0.012	11.11	3.32	3.34	139.59	171.93	182.87	0.798	0.782	6.99	0	152.17
PL	9.57	7	1	1.95	0.056	2.45	9.55	9.57	15.43	86.15	87.15	0.678	0.738	3.90	0	9.57
BC	2.96	4	1	4.43	0.004	9.04	2.37	2.50	3.14	6.08	6.18	0.980	0.918	8.34	0	2.96
AB	2.83	23	1	15.45	0.004	11.61	2.47	2.58	2.98	3.95	87.15	0.928	1.000	12.52	0	2.83
TP	12.78	232	1	29.24	0.004	7.42	6.72	7.70	12.14	28.60	29.93	0.996	1.000	7.53	1	12.78
RS	85.15	20	2	8.74	0.036	3.48	4.61	4.66	85.10	86.15	87.15	0.610	0.826	4.61	0	85.15

Table S 3.3. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream mean annual rainfall (U_MeanAnnRain) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	5000.34	87	1	16.48	0.008	5.27	3487.11	3688.92	5002.91	5113.81	5279.96	0.994	1.000	5.86	1	5000.34
GU	5193.34	77	1	12.69	0.020	3.04	1099.09	1099.60	4511.45	5193.76	5224.12	0.890	0.974	4.26	0	5193.34
CM	3393.25	11	1	3.81	0.004	6.25	1014.07	1069.70	3377.17	3420.85	3439.60	1.000	0.990	6.45	1	3393.25
CL	3394.82	4	1	1.38	0.056	2.32	2839.59	2917.35	3399.75	3455.10	3478.86	0.936	0.530	2.65	0	3394.82
WM	2373.48	65	1	20.48	0.004	14.68	1745.73	2086.95	2344.20	2553.12	2594.00	1.000	1.000	15.19	1	2373.48
TI	2789.85	27	1	13.57	0.004	18.19	1213.93	1350.27	2550.73	2774.32	2802.62	1.000	1.000	19.14	1	2789.85
CC	1648.75	7	1	3.03	0.120	2.43	1644.53	1647.78	2872.52	4216.89	4240.23	0.954	0.712	3.75	0	1648.75
LB	2753.10	4	1	2.07	0.004	4.86	1920.46	2014.34	2712.04	2763.18	2792.94	0.982	0.822	5.42	0	2753.10
SB	3795.55	4	1	1.14	0.136	1.54	2342.10	2396.53	3713.19	3843.17	3920.51	0.650	0.306	1.95	0	3795.55
PL	1201.60	7	1	12.52	0.012	6.04	1141.08	1201.60	1975.60	2335.89	3941.55	0.984	0.918	7.48	0	1201.60
BC	3414.77	4	1	1.36	0.064	2.30	2845.17	2927.40	3414.37	3471.58	3497.52	0.932	0.472	2.49	0	3414.77
AB	2017.18	23	1	7.71	0.004	5.52	1976.09	2015.96	2058.06	3484.73	5539.80	0.912	0.960	5.96	0	2017.18
TP	2472.56	232	2	29.95	0.004	6.93	1973.70	2026.95	2611.53	3002.91	4546.29	1.000	1.000	7.79	2	2472.56
RS	2706.53	20	1	4.98	0.012	4.63	2123.32	2147.64	2635.77	3493.91	3914.78	0.984	0.946	5.67	0	2706.53

Table S 3.4. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream maximum annual rainfall (U_MaxAnnRain) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	8920.75	87	2	20.50	0.004	3.44	2032.93	2867.67	8298.98	9296.21	9296.21	0.824	0.982	4.43	0	8920.75
GU	8920.75	77	2	24.54	0.004	5.81	2764.12	2807.99	8545.30	9296.21	9296.21	0.986	0.992	6.12	2	8920.75
CM	1274.61	11	1	23.41	0.076	3.58	1213.14	1213.14	3750.21	9809.79	9809.79	0.722	0.794	4.91	0	1274.61
CL	3750.20	4	2	1.02	0.284	1.20	3750.21	3819.23	4858.79	5636.96	5672.30	0.448	0.252	1.69	0	3750.20
WM	3886.34	65	1	15.47	0.004	11.50	1640.74	2509.08	3276.64	3918.50	3918.50	1.000	1.000	12.46	1	3886.34
TI	1603.25	27	1	40.53	0.004	16.49	1383.54	1400.60	1641.01	2316.12	2455.68	1.000	1.000	17.87	1	1603.25
CC	2015.80	7	1	4.36	0.068	3.35	1739.67	1784.30	2015.80	5521.39	5878.51	0.834	0.636	4.15	0	2015.80
LB	3713.23	4	1	2.22	0.012	4.60	2517.65	2567.97	3707.07	3729.96	3749.74	0.986	0.828	5.40	0	3713.23
SB	9989.51	4	2	39.66	0.004	14.62	4150.13	4778.46	9899.65	9989.51	9989.51	0.896	0.884	11.92	0	9989.51
PL	3258.46	7	1	2.93	0.008	4.60	2735.01	3108.55	3267.55	5636.96	5672.30	0.976	0.828	4.75	0	3258.46
BC	3887.55	4	1	1.16	0.016	1.63	3797.50	3819.23	3887.55	5811.75	5811.97	0.700	0.382	2.13	0	3887.55
AB	9989.51	23	2	36.71	0.024	4.83	1892.91	2646.53	9296.21	9989.51	9989.51	0.666	0.944	6.42	0	9989.51
TP	2858.53	232	2	33.84	0.004	7.75	2447.29	2455.68	2819.66	3109.66	3160.60	1.000	1.000	8.09	2	2858.53
RS	2542.87	20	1	7.52	0.004	5.80	2530.71	2535.91	3058.00	5940.05	6048.75	1.000	0.996	6.77	1	2542.87

Table S 3.5. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of local minimum reach elevation (L_MinEle) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	209.00	87	1	16.76	0.004	7.53	57.00	60.00	194.50	216.00	216.50	0.996	1.000	8.01	1	209.00
GU	229.00	77	1	14.66	0.004	5.55	27.50	30.50	219.50	232.65	238.50	1.000	0.998	5.87	1	229.00
CM	28.00	11	1	6.32	0.004	11.40	0.00	1.00	24.00	29.50	30.50	1.000	1.000	11.67	1	28.00
CL	24.00	4	1	1.68	0.040	2.82	7.50	9.00	23.50	205.50	208.50	0.836	0.636	4.39	0	24.00
WM	209.00	65	1	11.81	0.004	5.48	0.00	5.00	196.25	210.00	211.00	0.964	0.996	6.19	1	209.00
TI	3.00	27	1	28.72	0.004	23.62	0.00	0.00	3.00	8.00	9.00	1.000	1.000	24.25	1	3.00
CC	21.00	7	1	2.38	0.044	2.91	7.00	8.00	22.00	113.25	213.05	0.904	0.688	3.50	0	21.00
LB	99.50	4	1	1.20	0.092	1.93	33.00	37.45	92.50	107.00	114.50	0.878	0.406	2.21	0	99.50
SB	168.00	4	1	1.04	0.284	1.16	21.00	24.00	78.00	180.20	188.03	0.662	0.222	1.81	0	168.00
PL	402.50	7	2	4.94	0.060	3.77	39.00	122.90	402.75	555.10	566.00	0.956	0.736	4.89	0	402.50
BC	56.50	4	1	0.89	0.280	0.85	7.50	8.00	41.50	214.50	215.50	0.690	0.414	2.36	0	56.50
AB	647.00	23	2	63.28	0.012	6.04	3.98	8.00	27.00	647.00	647.00	0.460	0.978	8.41	0	647.00
TP	80.00	232	1	37.22	0.004	13.66	51.00	55.00	118.00	207.50	211.00	1.000	1.000	14.66	1	80.00
RS	509.50	20	2	9.29	0.080	3.47	0.00	9.00	447.50	535.00	553.50	0.838	0.796	4.36	0	509.50

Table S 3.6. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream mean air temperature (U_MeanTemp) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	20.62	87	2	24.96	0.004	19.86	20.40	20.52	21.43	21.67	21.85	1.000	1.000	20.57	2	20.62
GU	20.62	77	2	17.78	0.004	11.73	20.37	20.48	20.87	22.04	22.10	1.000	1.000	12.59	2	20.62
CM	21.61	11	2	5.92	0.004	9.31	21.59	21.63	21.70	21.98	22.22	0.994	0.982	9.41	2	21.61
CL	22.33	4	2	4.04	0.004	8.53	20.68	20.72	22.48	22.56	22.58	0.972	0.872	9.12	0	22.33
WM	22.95	65	2	49.23	0.004	16.81	20.79	21.39	22.87	23.03	23.09	1.000	1.000	17.45	2	22.95
TI	23.65	27	2	63.24	0.004	20.90	21.46	21.74	22.66	23.60	23.62	1.000	1.000	23.53	2	23.65
CC	21.90	7	2	5.52	0.004	9.38	20.85	21.85	22.00	22.58	22.65	1.000	0.988	11.05	2	21.90
LB	22.31	4	2	3.93	0.004	8.70	21.47	21.59	22.06	22.56	22.58	0.968	0.906	8.41	0	22.31
SB	20.37	4	2	1.60	0.020	3.38	20.03	20.22	20.38	21.99	22.06	0.956	0.666	3.56	0	20.37
PL	18.17	7	1	1.71	0.092	1.84	17.82	17.85	18.92	23.09	23.10	0.556	0.676	3.81	0	18.17
BC	21.93	4	2	2.69	0.012	5.55	20.71	20.78	21.96	22.52	22.54	0.966	0.820	6.44	0	21.93
AB	12.67	23	1	46.66	0.012	5.57	12.45	12.45	12.76	22.58	22.59	0.544	0.968	7.47	0	12.67
TP	13.99	232	2	40.85	0.008	4.33	13.99	13.99	16.04	22.77	22.94	0.652	1.000	5.07	0	13.99
RS	20.78	20	2	4.59	0.004	4.36	18.04	18.18	20.91	22.58	22.59	0.986	0.936	5.37	0	20.78

Table S 3.7. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of local percent open water (L_OpenWater) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.00	87	1	19.86	0.004	9.15	0.00	0.00	0.01	0.45	0.75	1.000	1.000	9.61	1	0.00
GU	0.06	77	1	14.19	0.004	8.33	0.00	0.00	0.01	0.06	0.07	1.000	1.000	8.52	1	0.06
CM	0.00	11	1	2.43	0.064	1.84	0.00	0.00	0.24	2.23	5.88	0.448	0.488	2.51	0	0.00
CL	0.00	4	1	9.51	0.032	5.88	0.00	0.00	0.00	0.00	0.00	0.964	0.740	4.35	0	0.00
WM	0.00	65	1	9.82	0.012	3.88	0.00	0.00	0.13	1.20	4.16	1.000	0.988	4.89	1	0.00
TI	0.10	27	2	7.14	0.004	7.40	0.02	0.03	0.12	0.47	1.16	0.998	0.996	8.26	2	0.10
CC	0.14	7	1	2.02	0.012	3.25	0.00	0.00	0.06	0.14	0.14	0.990	0.778	3.73	0	0.14
LB	0.00	4	1	2.07	0.060	3.67	0.00	0.00	0.00	0.74	0.86	0.604	0.286	1.88	0	0.00
SB	0.21	4	2	1.72	0.020	3.82	0.12	0.14	0.22	0.55	2.99	0.950	0.724	3.87	0	0.21
PL	0.00	7	1	3.76	0.004	4.14	0.00	0.00	0.00	0.10	0.12	0.994	0.872	4.37	0	0.00
BC	0.00	4	1	2.35	0.008	4.58	0.00	0.00	0.00	0.00	0.00	0.974	0.752	4.22	0	0.00
AB	0.00	23	1	29.97	0.100	2.80	0.00	0.00	0.08	16.52	16.83	0.476	0.590	2.66	0	0.00
TP	4.39	232	1	35.24	0.004	5.71	0.00	0.00	5.28	8.05	8.80	0.992	1.000	6.36	1	4.39
RS	0.03	20	1	4.65	0.004	4.99	0.00	0.00	0.22	0.57	0.63	1.000	0.998	5.49	1	0.03

Table S 3.8. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream percent open water (D_OpenWater) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	1.14	87	1	13.69	0.004	5.34	0.23	0.24	1.12	1.21	1.50	0.990	0.994	6.00	1	1.14
GU	0.41	77	1	11.94	0.004	5.16	0.00	0.16	0.41	1.43	1.60	1.000	1.000	6.44	1	0.41
CM	3.12	11	2	5.51	0.004	6.12	0.52	2.83	3.33	4.62	6.17	0.972	0.890	6.79	0	3.12
CL	8.76	4	2	5.08	0.100	3.06	0.12	0.26	3.25	8.02	8.76	0.774	0.554	3.96	0	8.76
WM	1.22	65	1	10.63	0.004	4.93	0.00	0.01	1.12	6.76	7.05	0.892	0.998	5.95	0	1.22
TI	2.30	27	2	7.19	0.004	5.15	0.68	0.73	2.34	6.81	7.03	0.978	0.976	6.67	2	2.30
CC	6.72	7	2	3.16	0.212	1.63	0.12	0.24	1.17	8.02	8.76	0.564	0.520	2.81	0	6.72
LB	0.70	4	2	1.37	0.028	2.69	0.60	0.68	0.79	0.96	1.40	0.968	0.546	2.60	0	0.70
SB	3.19	4	2	3.04	0.008	6.76	2.06	2.11	2.36	3.69	3.87	0.984	0.926	7.87	0	3.19
PL	0.83	7	1	2.24	0.016	3.66	0.02	0.04	0.48	0.87	0.90	1.000	0.926	4.45	0	0.83
BC	2.36	4	2	2.30	0.024	3.89	0.31	0.85	2.36	7.82	8.02	0.922	0.730	5.57	0	2.36
AB	1.44	23	1	3.59	0.092	1.54	0.00	0.00	0.74	1.48	2.36	0.708	0.750	3.24	0	1.44
TP	4.48	232	1	31.72	0.004	4.44	0.14	0.36	4.49	5.00	5.04	0.876	0.994	5.04	0	4.48
RS	10.38	20	2	15.53	0.044	3.78	0.05	0.37	8.71	12.10	12.67	0.550	0.884	4.80	0	10.38

Table S 3.9. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream maximum soil permeability (U_MaxSoilPerm) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	4.00	87	1	31.73	0.004	22.84	4.00	4.00	4.00	4.82	5.24	1.000	1.000	22.48	1	4.00
GU	4.39	77	1	19.32	0.004	11.48	4.00	4.00	4.00	4.66	4.82	0.998	1.000	12.28	1	4.39
CM	4.00	11	1	2.48	0.108	1.94	4.00	4.00	4.00	20.00	20.00	0.702	0.582	3.22	0	4.00
CL	4.82	4	1	2.31	0.008	5.21	4.00	4.00	4.00	4.00	4.74	0.978	0.904	6.96	0	4.82
WM	4.00	65	1	16.19	0.004	10.79	4.00	4.00	4.00	5.24	5.24	1.000	1.000	10.83	1	4.00
TI	13.00	27	1	4.88	0.024	2.33	4.00	4.00	11.00	13.00	17.08	0.856	0.630	2.62	0	13.00
CC	4.00	7	1	5.06	0.004	8.84	4.00	4.00	4.00	4.78	5.22	1.000	0.992	9.12	1	4.00
LB	4.00	4	1	2.37	0.012	4.77	4.00	4.00	4.00	13.00	13.00	0.912	0.674	5.02	0	4.00
SB	13.00	4	2	1.08	0.304	1.41	4.00	4.00	13.00	13.00	13.00	0.542	0.304	2.05	0	13.00
PL	4.00	7	1	3.69	0.092	2.79	4.00	4.00	11.00	17.08	17.08	0.574	0.552	3.38	0	4.00
BC	4.00	4	1	2.88	0.004	5.70	4.00	4.00	4.00	4.25	4.78	0.990	0.894	6.84	0	4.00
AB	4.00	23	1	5.38	0.020	2.33	4.00	4.00	5.24	20.00	20.00	0.734	0.592	2.75	0	4.00
TP	13.00	232	1	25.54	0.008	3.49	4.00	4.00	11.50	13.00	20.00	0.838	0.904	3.73	0	13.00
RS	4.00	20	1	4.21	0.156	1.19	4.00	4.00	9.01	13.00	17.08	0.586	0.612	2.72	0	4.00

Table S 3.10. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream minimum soil permeability (U_MinSoilPerm) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	**zenv. cp**	**freq**	**max grp**	**Ind Val**	**obsiv. prob**	**z score**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z. median**	**filter**	**zenv. cp**
GS	3.60	87	1	17.19	0.004	9.56	0.70	0.81	2.85	4.00	4.00	1.000	1.000	9.73	1	3.60
GU	4.00	77	1	13.82	0.060	2.14	0.00	0.00	1.30	4.00	4.00	0.840	0.750	2.65	0	4.00
CM	0.70	11	1	3.78	0.004	6.33	0.00	0.05	0.70	0.70	0.70	1.000	0.992	7.46	1	0.70
CL	0.70	4	1	1.86	0.008	5.18	0.00	0.00	0.35	0.70	0.83	0.986	0.812	4.64	0	0.70
WM	4.00	65	1	9.97	0.004	3.89	0.00	0.70	3.50	4.00	4.00	0.842	0.990	4.65	0	4.00
TI	0.70	27	1	9.63	0.004	10.86	0.21	0.33	0.70	0.92	1.30	1.000	1.000	11.87	1	0.70
CC	0.70	7	1	2.72	0.004	5.06	0.00	0.00	0.70	0.88	0.92	1.000	0.966	5.83	1	0.70
LB	0.00	4	1	2.87	0.164	2.11	0.00	0.00	0.00	1.30	2.11	0.856	0.432	2.60	0	0.00
SB	0.00	4	1	2.72	0.008	5.61	0.00	0.00	0.00	0.05	0.05	0.978	0.896	6.94	0	0.00
PL	0.35	7	2	1.73	0.084	1.88	0.35	0.70	0.70	1.30	2.85	0.678	0.622	2.66	0	0.35
BC	0.00	4	1	3.37	0.012	6.20	0.00	0.00	0.00	0.70	0.83	0.974	0.842	5.20	0	0.00
AB	0.92	23	1	5.63	0.004	5.83	0.00	0.00	0.53	1.30	2.64	0.998	0.994	7.13	1	0.92
TP	0.70	232	2	24.57	0.024	2.89	0.00	0.32	0.70	4.00	4.00	0.566	0.932	3.37	0	0.70
RS	2.85	20	1	4.54	0.008	4.00	0.00	0.92	3.30	4.00	4.00	0.890	0.946	4.29	0	2.85

Table S 3.11. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream range of mean annual rainfall (U_RanAnnRain) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	614.93	87	2	16.36	0.004	8.73	466.28	563.36	615.36	638.36	651.64	0.994	1.000	8.79	2	614.93
GU	465.19	77	2	14.28	0.004	6.31	325.78	338.71	469.93	800.45	807.75	1.000	1.000	7.08	2	465.19
CM	579.43	11	2	2.17	0.084	1.79	174.42	175.27	582.46	998.84	1570.28	0.504	0.720	3.15	0	579.43
CL	777.02	4	2	1.25	0.108	2.03	745.99	762.09	842.55	2824.49	2869.38	0.890	0.420	2.54	0	777.02
WM	994.28	65	1	10.67	0.004	5.20	114.77	114.77	930.51	1696.24	1767.15	0.998	0.998	6.60	1	994.28
TI	695.01	27	1	7.20	0.004	7.51	114.77	114.81	536.56	861.15	885.24	1.000	1.000	9.40	1	695.01
CC	1834.45	7	1	1.47	0.352	0.70	278.45	280.30	869.88	1285.68	1368.90	0.524	0.406	2.21	0	1834.45
LB	628.35	4	1	1.86	0.016	4.21	271.44	287.44	441.27	636.57	654.12	0.982	0.820	5.11	0	628.35
SB	1103.52	4	1	1.11	0.144	1.54	369.81	384.85	928.68	1122.30	1147.83	0.768	0.252	1.91	0	1103.52
PL	691.33	7	2	2.01	0.032	3.09	702.20	708.73	747.57	1001.66	1092.94	0.786	0.752	3.28	0	691.33
BC	817.38	4	2	1.28	0.112	2.09	704.98	756.95	821.22	1221.98	1717.71	0.760	0.402	2.31	0	817.38
AB	472.56	23	1	3.82	0.104	1.70	376.28	405.04	495.74	3144.68	3158.04	0.594	0.740	3.31	0	472.56
TP	2454.93	232	1	29.74	0.012	3.53	277.43	287.06	2420.72	3162.42	3173.41	0.534	0.998	4.85	0	2454.93
RS	745.58	20	1	4.01	0.012	3.27	114.77	114.81	680.31	881.46	914.98	0.838	0.850	4.29	0	745.58

Table S 3.12. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream shrubland (U_Shrub) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	9.78	87	2	18.28	0.004	10.36	9.50	9.62	9.84	11.86	11.97	1.000	1.000	11.55	2	9.78
GU	9.70	77	2	13.42	0.004	6.83	6.15	9.13	9.72	12.24	29.74	1.000	1.000	7.55	2	9.70
CM	51.97	11	2	9.16	0.004	5.58	10.71	11.16	28.85	53.92	53.99	0.998	0.952	6.56	2	51.97
CL	53.67	4	2	12.16	0.008	7.42	12.32	12.56	53.14	55.71	56.80	0.964	0.796	7.83	0	53.67
WM	1.15	65	2	12.08	0.048	2.50	1.07	1.13	1.70	29.81	53.91	0.642	0.944	3.21	0	1.15
TI	7.55	27	2	3.90	0.120	1.44	2.86	3.31	10.67	32.18	42.74	0.794	0.748	2.97	0	7.55
CC	53.99	7	2	6.24	0.004	2.39	1.12	1.14	16.15	53.91	53.99	0.690	0.578	3.05	0	53.99
LB	28.73	4	2	1.96	0.076	3.01	8.27	9.07	26.77	29.25	29.38	0.916	0.592	3.99	0	28.73
SB	26.16	4	2	2.13	0.028	3.90	14.53	14.77	25.96	28.50	32.29	0.972	0.786	5.16	0	26.16
PL	1.70	7	1	3.35	0.032	3.62	1.39	1.50	1.82	10.56	21.44	0.958	0.774	4.60	0	1.70
BC	53.06	4	2	17.47	0.004	12.82	13.23	42.54	53.67	56.82	62.04	0.968	0.934	13.53	0	53.06
AB	9.27	23	2	5.08	0.004	5.10	8.91	9.09	9.65	12.18	14.29	0.960	0.954	4.92	2	9.27
TP	0.10	232	2	39.93	0.040	2.20	0.09	0.13	11.88	33.68	53.75	0.884	0.934	3.49	0	0.10
RS	16.19	20	1	3.26	0.068	1.84	3.39	3.59	14.40	21.67	21.85	0.724	0.848	3.10	0	16.19

Table S 3.13. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream shrubland (D_Shrub) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	5.40	87	2	12.75	0.012	3.54	1.36	1.40	5.39	23.20	29.72	0.808	0.972	4.07	0	5.40
GU	5.39	77	2	12.79	0.004	4.69	2.66	3.23	5.48	8.94	14.25	0.960	0.996	5.38	2	5.39
CM	2.24	11	1	2.48	0.204	1.10	1.22	1.46	7.01	22.14	22.42	0.572	0.724	3.65	0	2.24
CL	6.42	4	2	1.02	0.240	1.12	6.39	6.51	12.20	25.77	26.07	0.664	0.300	1.91	0	6.42
WM	13.31	65	1	7.95	0.088	1.43	1.58	3.28	13.29	36.21	46.08	0.480	0.838	3.15	0	13.31
TI	0.76	27	2	4.86	0.408	0.45	1.81	2.32	9.11	21.24	22.82	0.462	0.548	2.34	0	0.76
CC	13.70	7	1	1.78	0.100	1.94	6.48	6.75	11.79	13.80	14.01	0.792	0.564	2.59	0	13.70
LB	10.44	4	1	1.25	0.092	2.00	3.17	3.58	10.38	11.04	11.46	0.802	0.368	2.21	0	10.44
SB	7.36	4	2	1.14	0.104	1.76	6.71	7.25	8.04	9.34	12.98	0.570	0.282	2.00	0	7.36
PL	9.96	7	2	1.87	0.016	2.57	7.20	9.40	10.38	31.78	32.86	0.786	0.688	3.33	0	9.96
BC	23.55	4	2	2.07	0.076	3.58	6.50	6.96	25.42	35.91	37.27	0.910	0.598	4.25	0	23.55
AB	3.81	23	2	4.21	0.048	2.25	3.81	3.97	7.48	19.62	22.70	0.636	0.900	3.30	0	3.81
TP	9.19	232	2	23.17	0.044	1.72	0.00	0.51	11.18	42.99	43.09	0.620	0.886	3.23	0	9.19
RS	3.37	20	1	3.06	0.212	0.81	2.33	2.97	10.04	29.83	30.20	0.658	0.634	2.73	0	3.37

Table S 3.14. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream population density (U_Pop) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	3.76	87	2	22.00	0.004	15.03	2.11	3.03	4.16	4.86	5.75	1.000	1.000	15.84	2	3.76
GU	4.17	77	2	19.08	0.004	12.99	3.64	3.89	5.00	8.60	9.14	1.000	1.000	14.16	2	4.17
CM	25.68	11	2	7.42	0.004	8.88	9.76	10.71	24.75	77.34	104.07	0.980	1.000	10.59	2	25.68
CL	20.07	4	2	2.67	0.004	6.62	0.03	0.03	19.71	61.97	64.11	0.842	0.814	6.43	0	20.07
WM	23.14	65	2	30.47	0.004	19.21	11.44	12.58	22.18	26.99	40.76	1.000	1.000	20.04	2	23.14
TI	131.09	27	2	39.61	0.004	25.08	58.50	91.75	156.67	567.88	597.79	1.000	1.000	26.19	2	131.09
CC	40.86	7	2	7.57	0.004	9.70	13.13	17.27	43.56	169.98	186.51	1.000	0.994	11.67	2	40.86
LB	101.81	4	2	2.18	0.200	1.51	0.32	0.33	10.32	140.10	142.23	0.806	0.426	2.44	0	101.81
SB	0.00	4	1	9.66	0.004	6.62	0.00	0.00	0.00	0.82	8.86	0.886	0.798	8.82	0	0.00
PL	27.98	7	2	4.67	0.004	5.75	0.03	0.04	26.97	43.53	43.56	0.820	0.952	7.44	0	27.98
BC	34.25	4	2	4.04	0.004	8.88	4.24	4.66	40.80	49.79	60.43	0.988	0.870	8.64	0	34.25
AB	42.78	23	2	9.09	0.004	5.44	0.00	0.01	43.54	168.52	171.90	0.820	0.956	6.39	0	42.78
TP	101.81	232	1	32.84	0.012	3.27	0.01	0.10	117.75	150.03	168.76	0.866	0.970	4.00	0	101.81
RS	516.61	20	2	16.20	0.016	5.54	0.32	0.80	25.40	679.08	761.88	0.958	0.994	7.96	2	516.61

Table S 3.15. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream road length density (U_RoadLen) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	**zenv. cp**	**freq**	**max grp**	**Ind Val**	**obsiv. prob**	**z score**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z. median**	**filter**	**zenv. cp**
GS	0.00	87	1	15.06	0.008	4.02	0.00	0.00	6.62	7.33	12.45	0.362	0.928	5.07	0	0.00
GU	7.08	77	2	37.48	0.004	6.95	1.25	1.44	6.37	7.09	7.28	0.988	0.996	7.76	2	7.08
CM	0.21	11	2	3.07	0.012	4.15	0.20	0.20	0.22	0.40	0.47	0.992	0.954	4.22	2	0.21
CL	0.34	4	2	1.30	0.108	2.15	0.27	0.29	0.33	0.57	0.61	0.906	0.404	2.30	0	0.34
WM	1.67	65	2	19.36	0.004	12.09	0.86	0.96	1.67	5.38	6.00	1.000	1.000	13.41	2	1.67
TI	2.26	27	2	14.99	0.004	15.30	1.67	1.71	2.41	9.13	9.32	1.000	1.000	17.07	2	2.26
CC	5.41	7	2	6.11	0.012	4.06	0.47	0.47	4.33	5.48	5.57	0.976	0.842	5.10	0	5.41
LB	0.77	4	2	2.06	0.012	4.56	0.75	0.78	1.93	6.39	6.53	0.984	0.856	6.35	0	0.77
SB	0.31	4	2	1.27	0.096	2.19	0.29	0.31	0.52	0.92	2.60	0.952	0.534	2.98	0	0.31
PL	0.00	7	1	5.36	0.156	2.03	0.00	0.00	0.22	1.54	1.71	0.536	0.528	2.92	0	0.00
BC	0.62	4	1	1.06	0.292	1.24	0.00	0.00	0.33	0.64	0.67	0.610	0.340	2.19	0	0.62
AB	0.41	23	2	4.54	0.004	3.81	0.07	0.10	0.48	7.86	8.61	0.990	0.954	5.20	2	0.41
TP	2.29	232	1	26.54	0.024	2.92	0.00	0.00	0.80	2.67	7.32	0.952	0.968	4.05	1	2.29
RS	6.73	20	2	18.58	0.004	8.02	0.26	0.27	5.35	10.05	11.01	1.000	1.000	9.16	2	6.73

Table S 3.16. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream density of ICIS sites (D_ICIS) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.23	87	2	26.80	0.004	8.57	0.00	0.12	0.23	1.31	1.31	0.984	0.998	8.93	2	0.23
GU	1.05	77	2	40.76	0.004	10.89	0.00	0.00	0.62	1.26	1.26	1.000	1.000	12.18	2	1.05
CM	0.00	11	1	2.29	0.212	1.26	0.00	0.00	0.00	0.00	0.00	0.756	0.414	2.24	0	0.00
CL	0.00	4	2	0.99	0.292	0.93	0.00	0.00	0.00	0.00	0.00	0.326	0.286	1.87	0	0.00
WM	0.47	65	2	33.16	0.004	12.81	0.20	0.23	0.32	1.30	1.31	0.998	0.998	12.57	2	0.47
TI	0.12	27	2	15.16	0.004	9.63	0.00	0.12	0.47	2.04	2.67	0.990	0.986	11.28	2	0.12
CC	3.34	7	2	15.70	0.004	4.65	0.00	0.00	1.83	3.74	3.74	0.814	0.716	5.66	0	3.34
LB	0.00	4	1	1.10	0.172	1.61	0.00	0.00	0.00	0.00	0.00	0.634	0.288	1.98	0	0.00
SB	0.00	4	2	3.66	0.004	8.43	0.00	0.00	0.00	0.11	0.12	0.948	0.806	8.00	0	0.00
PL	0.00	7	1	6.35	0.020	5.32	0.00	0.00	0.00	0.00	0.00	0.722	0.352	2.07	0	0.00
BC	0.00	4	1	0.82	0.568	-0.01	0.00	0.00	0.00	0.00	0.00	0.606	0.262	1.69	0	0.00
AB	0.00	23	2	4.45	0.020	3.13	0.00	0.00	0.01	3.34	3.42	0.820	0.780	4.61	0	0.00
TP	0.00	232	1	33.65	0.004	5.37	0.00	0.00	0.00	0.12	0.56	0.954	0.998	5.04	1	0.00
RS	0.13	20	2	11.42	0.004	7.37	0.00	0.00	0.12	0.31	0.38	0.962	0.946	7.50	0	0.13

Table S 3.17. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream ditch length (D_DitchLen) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	699.31	87	2	18.77	0.004	8.87	163.56	212.96	659.25	1862.15	1878.58	1.000	1.000	9.73	2	699.31
GU	1636.30	77	2	54.78	0.004	17.19	819.14	845.42	1176.13	1798.09	1825.41	1.000	1.000	18.46	2	1636.30
CM	0.00	11	1	2.39	0.136	1.35	0.00	0.00	0.00	1010.62	1231.70	0.634	0.546	2.81	0	0.00
CL	0.00	4	2	1.08	0.272	1.39	0.00	0.00	0.00	432.75	493.36	0.180	0.404	2.43	0	0.00
WM	1811.68	65	2	41.82	0.004	9.54	30.02	206.67	1658.40	1914.64	1942.82	0.998	1.000	11.24	2	1811.68
TI	0.00	27	2	4.21	0.040	1.99	0.00	0.00	163.18	2001.81	2015.74	0.868	0.800	3.97	0	0.00
CC	0.00	7	2	1.78	0.076	2.06	0.00	0.00	698.45	1469.49	1486.30	0.680	0.532	3.24	0	0.00
LB	1218.63	4	2	3.74	0.012	5.85	0.00	36.80	1220.07	1547.27	1580.32	0.964	0.748	5.26	0	1218.63
SB	23.20	4	2	1.41	0.040	2.53	0.00	0.00	16.49	312.04	342.63	0.956	0.568	2.81	0	23.20
PL	1135.27	7	2	2.49	0.132	1.67	0.00	0.00	555.40	1141.53	1205.45	0.772	0.570	3.42	0	1135.27
BC	0.00	4	2	0.97	0.332	0.88	0.00	0.00	0.00	672.19	723.13	0.210	0.362	2.36	0	0.00
AB	0.00	23	2	3.03	0.292	0.61	0.00	0.00	228.23	1858.13	1899.04	0.530	0.530	2.61	0	0.00
TP	0.00	232	1	29.15	0.008	4.27	0.00	0.00	469.47	1953.31	2126.34	0.518	0.908	3.40	0	0.00
RS	228.82	20	2	6.97	0.004	9.64	228.54	237.41	477.97	661.45	716.03	1.000	0.998	10.95	2	228.82

Table S 3.18. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream density of ditch intersections (D_DitchX) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.12	87	2	12.61	0.016	3.25	0.00	0.00	0.19	2.29	2.38	0.882	0.902	4.58	0	0.12
GU	0.12	77	2	21.70	0.004	11.51	0.11	0.11	0.17	2.18	2.33	1.000	1.000	12.74	2	0.12
CM	0.00	11	1	2.51	0.036	2.66	0.00	0.00	0.00	0.00	0.00	0.950	0.664	3.21	0	0.00
CL	0.00	4	2	1.16	0.120	1.79	0.00	0.00	0.00	0.12	0.14	0.490	0.270	1.97	0	0.00
WM	0.14	65	2	13.24	0.004	5.41	0.00	0.00	0.15	0.36	4.41	0.944	0.946	5.77	0	0.14
TI	0.00	27	1	10.89	0.264	1.42	0.00	0.00	0.00	0.19	0.57	0.758	0.558	2.51	0	0.00
CC	0.00	7	2	1.55	0.340	1.06	0.00	0.00	0.00	0.36	0.43	0.510	0.424	2.60	0	0.00
LB	0.15	4	2	2.64	0.012	4.96	0.00	0.00	0.15	0.50	0.60	0.920	0.794	6.13	0	0.15
SB	0.00	4	2	1.47	0.052	2.68	0.00	0.00	0.00	0.28	0.30	0.500	0.314	2.13	0	0.00
PL	0.00	7	1	1.65	0.024	2.02	0.00	0.00	0.00	0.32	0.32	0.464	0.492	2.80	0	0.00
BC	0.00	4	2	1.12	0.140	1.71	0.00	0.00	0.00	0.09	0.12	0.422	0.288	1.95	0	0.00
AB	0.00	23	2	4.20	0.048	2.25	0.00	0.00	0.00	0.39	0.42	0.688	0.638	2.95	0	0.00
TP	0.00	232	1	28.85	0.004	5.71	0.00	0.00	0.00	2.03	2.19	0.748	0.994	5.48	0	0.00
RS	0.56	20	2	5.14	0.132	1.56	0.00	0.00	0.05	0.57	0.63	0.654	0.606	3.11	0	0.56

Table S 3.19. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream pipeline length (U_PipeLen) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.00	87	1	15.91	0.028	1.98	0.00	0.00	0.00	1024.20	1024.20	0.242	0.806	3.56	0	0.00
GU	0.00	77	1	9.51	0.088	1.68	0.00	0.00	0.00	0.00	31.30	0.414	0.680	2.97	0	0.00
CM	0.00	11	1	1.57	0.384	0.27	0.00	0.00	0.00	0.00	0.00	0.664	0.366	2.11	0	0.00
CL	0.00	4	2	2.04	0.072	3.10	0.00	0.00	0.00	0.00	0.00	0.414	0.296	2.12	0	0.00
WM	153.82	65	2	14.39	0.020	2.26	0.00	0.00	0.00	229.34	711.73	0.744	0.778	3.71	0	153.82
TI	0.00	27	2	13.14	0.004	5.60	0.00	0.00	180.18	468.15	713.23	0.932	0.900	6.69	0	0.00
CC	620.82	7	2	7.41	0.108	2.93	0.00	0.00	0.00	711.73	711.73	0.712	0.482	3.42	0	620.82
LB	0.00	4	2	0.98	0.324	0.77	0.00	0.00	0.00	0.00	0.00	0.430	0.292	1.96	0	0.00
SB	0.00	4	2	2.79	0.048	4.22	0.00	0.00	0.00	520.90	520.90	0.736	0.536	3.95	0	0.00
PL	0.00	7	2	1.94	0.048	2.47	0.00	0.00	0.00	216.08	228.22	0.626	0.534	3.20	0	0.00
BC	0.00	4	2	1.23	0.116	1.99	0.00	0.00	0.00	0.00	0.00	0.428	0.284	2.01	0	0.00
AB	0.00	23	1	6.04	0.020	3.24	0.00	0.00	0.00	1179.93	1179.93	0.408	0.590	3.08	0	0.00
TP	0.00	232	1	24.84	0.016	2.46	0.00	0.00	0.00	579.10	908.84	0.716	0.656	2.48	0	0.00
RS	0.00	20	2	3.31	0.068	1.62	0.00	0.00	0.00	135.03	153.82	0.598	0.602	2.94	0	0.00

Table S 3.20. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of local pipeline length (L_PipeLen) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.00	87	1	15.91	0.028	1.98	0.00	0.00	0.00	1024.20	1024.20	0.242	0.806	3.56	0	0.00
GU	0.00	77	1	9.51	0.088	1.68	0.00	0.00	0.00	0.00	31.30	0.414	0.680	2.97	0	0.00
CM	0.00	11	1	1.57	0.384	0.27	0.00	0.00	0.00	0.00	0.00	0.664	0.366	2.11	0	0.00
CL	0.00	4	2	2.04	0.072	3.10	0.00	0.00	0.00	0.00	0.00	0.414	0.296	2.12	0	0.00
WM	153.82	65	2	14.39	0.020	2.26	0.00	0.00	0.00	229.34	711.73	0.744	0.778	3.71	0	153.82
TI	0.00	27	2	13.14	0.004	5.60	0.00	0.00	180.18	468.15	713.23	0.932	0.900	6.69	0	0.00
CC	620.82	7	2	7.41	0.108	2.93	0.00	0.00	0.00	711.73	711.73	0.712	0.482	3.42	0	620.82
LB	0.00	4	2	0.98	0.324	0.77	0.00	0.00	0.00	0.00	0.00	0.430	0.292	1.96	0	0.00
SB	0.00	4	2	2.79	0.048	4.22	0.00	0.00	0.00	520.90	520.90	0.736	0.536	3.95	0	0.00
PL	0.00	7	2	1.94	0.048	2.47	0.00	0.00	0.00	216.08	228.22	0.626	0.534	3.20	0	0.00
BC	0.00	4	2	1.23	0.116	1.99	0.00	0.00	0.00	0.00	0.00	0.428	0.284	2.01	0	0.00
AB	0.00	23	1	6.04	0.020	3.24	0.00	0.00	0.00	1179.93	1179.93	0.408	0.590	3.08	0	0.00
TP	0.00	232	1	24.84	0.016	2.46	0.00	0.00	0.00	579.10	908.84	0.716	0.656	2.48	0	0.00
RS	0.00	20	2	3.31	0.068	1.62	0.00	0.00	0.00	135.03	153.82	0.598	0.602	2.94	0	0.00

Table S 3.21. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of upstream CERCLIS sites (U_CERCLIS) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.00	87	2	14.96	0.004	5.84	0.00	0.00	0.00	0.00	0.00	0.442	0.560	2.39	0	0.00
GU	0.00	77	2	12.09	0.016	2.72	0.00	0.00	0.00	0.00	0.00	0.422	0.572	2.51	0	0.00
CM	0.00	11	2	3.07	0.012	4.06	0.00	0.00	0.00	0.00	0.00	0.504	0.422	2.47	0	0.00
CL	0.00	4	2	1.10	0.164	1.37	0.00	0.00	0.00	0.00	0.00	0.482	0.314	2.26	0	0.00
WM	0.00	65	1	57.44	0.008	4.30	0.00	0.00	0.00	0.00	0.00	0.572	0.548	2.38	0	0.00
TI	0.04	27	2	96.08	0.004	11.30	0.00	0.00	0.00	0.04	0.07	0.958	0.930	10.54	0	0.04
CC	0.00	7	1	1.65	0.164	1.41	0.00	0.00	0.00	0.00	0.00	0.530	0.380	2.30	0	0.00
LB	0.00	4	1	2.30	0.012	4.74	0.00	0.00	0.00	0.00	0.00	0.496	0.356	2.40	0	0.00
SB	0.00	4	1	1.13	0.120	1.63	0.00	0.00	0.00	0.00	0.00	0.486	0.302	2.36	0	0.00
PL	0.00	7	1	24.02	0.036	5.49	0.00	0.00	0.00	0.00	0.00	0.522	0.370	2.43	0	0.00
BC	0.00	4	2	1.13	0.160	1.57	0.00	0.00	0.00	0.00	0.00	0.542	0.348	2.41	0	0.00
AB	0.00	23	1	29.97	0.116	2.81	0.00	0.00	0.00	0.00	0.00	0.578	0.488	2.50	0	0.00
TP	0.00	232	1	40.00	0.032	2.25	0.00	0.00	0.00	0.00	0.00	0.652	0.620	2.36	0	0.00
RS	0.00	20	2	6.68	0.308	0.69	0.00	0.00	0.00	0.00	0.00	0.460	0.484	2.56	0	0.00

Table S 3.22. TITAN environmental changing-points (zenv.cp) and bootstrap confidence intervals (median among 500 iterations) of downstream former plantation (D_FormPlan) on selected taxa using presence-absence at the reach-scale. Frequency (freq) indicates the number of occurrences per taxon. Maximum group (maxgrp) indicates the response direction, with 1 = negative (z-) and 2 = positive (z+). Indicator value (IndVal) is the IndVal statistic (Dufrene & Legendre 1997), scaled 0-100%. Observation probability (obsiv.prob) indicates the probability of obtaining an equal or larger IndVal score from random data. Z score is the corresponding z score for the Indicator value. Purity is the mean proportion of correct response direction (z-) or (z+) assignments, reliability is the mean proportion of p-values ≤ 0.05 among 500 iterations. The median z score (z.median) indicates the median z score magnitude across all bootstrap replicates, and filter is a logical (if >0) indicating whether each taxon met purity and reliability criteria (0.95 and 0.95 respectively), value indicates maxgrp assignment. GS = Green Swordtail, GU = Guppy, CM = Common Molly, CL = Cuban Limia, WM = Western Mosquitofish, TI = tilapia, CC = Convict Cichlid, LB = Largemouth Bass, SB = Smallmouth Bass, PL = Pond Loach, BC = Bristle-nosed Catfish, AB = American Bullfrog, TP = Tahitian Prawn, RS = Red Swamp Crayfish.

Taxa	zenv. cp	freq	max grp	Ind Val	obsiv. prob	z score	5%	10%	50%	90%	95%	purity	reliability	z. median	filter	zenv. cp
GS	0.00	87	1	20.82	0.012	3.95	0.00	0.00	0.00	35.54	43.84	0.754	0.712	2.90	0	0.00
GU	43.84	77	2	30.30	0.160	1.89	0.00	0.00	21.91	43.84	43.84	0.510	0.774	3.29	0	43.84
CM	0.00	11	1	4.88	0.024	3.90	0.00	0.00	0.00	0.00	0.00	0.806	0.444	2.31	0	0.00
CL	0.00	4	1	2.77	0.184	1.64	0.00	0.00	0.00	10.85	11.80	0.488	0.324	2.21	0	0.00
WM	35.90	65	2	22.13	0.116	1.90	0.00	0.00	1.38	35.90	37.88	0.738	0.820	3.78	0	35.90
TI	36.42	27	2	18.62	0.056	3.79	0.00	0.00	36.42	53.16	56.97	0.772	0.746	4.50	0	36.42
CC	0.00	7	1	5.47	0.044	4.07	0.00	0.00	23.21	43.84	43.84	0.222	0.684	5.18	0	0.00
LB	1.88	4	2	2.35	0.016	4.41	0.00	0.00	2.31	4.70	11.27	0.922	0.758	5.75	0	1.88
SB	2.43	4	2	3.54	0.008	8.29	0.00	0.00	2.59	4.41	4.93	0.990	0.908	8.26	0	2.43
PL	18.18	7	2	2.71	0.104	2.24	0.00	0.00	0.00	19.77	21.78	0.644	0.548	3.29	0	18.18
BC	40.75	4	2	16.17	0.032	5.88	0.00	0.00	37.60	43.84	43.84	0.704	0.686	5.98	0	40.75
AB	0.00	23	2	4.24	0.040	2.43	0.00	0.00	1.42	42.72	43.84	0.786	0.750	3.88	0	0.00
TP	0.00	232	1	24.58	0.024	2.46	0.00	0.00	0.00	32.40	33.33	0.632	0.694	2.69	0	0.00
RS	35.90	20	2	27.33	0.008	6.91	0.00	0.00	36.42	39.63	40.75	0.868	0.880	7.81	0	35.90

Chapter Four – Modeling the stream reach suitability of introduced species in Hawaiʻi

4.1 Introduction

Species and their associations with landscape environmental factors have been increasingly applied to freshwater systems to predict local biodiversity in areas where biological information is not available (Townsend et al. 2003, McNyset 2005, Oakes et al. 2005, Buisson et al. 2008, Maloney et al. 2013). This is done by developing species distribution models or suitability models that relate biological observations to environmental predictor variables, based on statistically or theoretically derived responses (Guisan & Zimmermann 2000). Ideal environmental predictors should reflect species response to physiological limitations, disturbances, and resources (Guisan & Thuiller 2005). These modeling approaches have been applied to describe the range of native freshwater species in large temperate continental regions. Similarly, species models have been applied to describe the range of native vegetation in Hawaiʻi (Fortini et al. 2013) but has not been applied to the freshwater species in Hawaiʻi.

Species models have been applied to introduced freshwater species to predict the various processes that occur with biological invasions including the risk of introduction, the establishment of reproducing populations, and the potential spread of established populations (Peterson 2003). Predicting the risk of introduction has generally been based on human-mediated factors (e.g., site accessibility), whereas the establishment and spread of species has been based on enviornmental factors (e.g., temperature). These models served as important resources to ecological managers, as the prevention of the introduction and establishment of introduced species is much more feasible and cost-effective compared to the control of established introduced species (Ficetola et al. 2007). For example, Sharma et al. (2009) predicted the risk of Smallmouth Bass (*Micropterus dolomieu*) introduction and establishment in British Columbia to facilitate the conservation of native salmonid species. Ecological niche models have been commonly applied to evaluate the potential distribution of introduced species in their non-native range to inform management plans (e.g., Zebra Mussels, Drake & Bossenbroek 2004; snakehead and Asian carp species, Ficetola et al. 2007; American Bullfrog, Herborg et al. 2007; carp, trout, and catfish species among others, Britton et al. 2010). In this study the stream reach suitability of species was modeled for selected introduced stream species based on their observed occurrences throughout Hawaiʻi (i.e., their non-native range). Therefore, based on where introduced species have occurred, we aimed to predict their suitable stream reaches based on their shown association with the environmental factors in Hawaiʻi. Due to the potential lack of species equilibrium for these species (i.e., species may have not reached all suitable locations), it is possible that the predicted range of suitable reaches based on the observed occurances was less comprehensive, or narrower, compared to the actual availability of all suitable reaches. However, the predicted stream reaches of these introduced species may provide a starting point to further investigate and revise our understanding of introduced species occupancy in Hawaiian streams.

The primary objective of Chapter Four was to describe the potential distributions of introduced species by predicting reach suitability in Hawaiian streams using landscape-scale environmental factors. Suitable stream reaches were defined as reaches with environmental characteristics that could support a given species. Through this investigation I aimed to answer the questions:

(1) What stream reaches exhibited the highest probabilities of suitability for the selected introduced taxa, and how did the spatial distribution of these reaches compare among taxa?

(2) Which taxa exhibited the greatest potential to expand their current range in Hawaiian streams, i.e., which taxa exhibited the greatest number reaches with high probabilities of suitability outside of their observed distribution?
(3) Were there spatial locations such as islands, regions (e.g., windward and leeward), or streams that generally exhibited high or low suitability probabilities among the taxa assessed?

Information on taxa observed stream reach occurrences versus suitable reaches aimed to inform managers of each taxon's potential to expand within the watersheds, and throughout the state if dispersal to previously uninhabited watersheds is facilitated. Collectively, the species models indicated the reaches, streams, and watersheds that exhibited the most (and least) potential to support the greatest number of introduced species. Information on the extent overlap between the suitable reaches of introduced species and native species distributions should allow managers to prioritize streams and watersheds for conservation and restoration.

4.2 Methods

4.2.1 Study design and taxa selection

Species suitability models were created for taxa with ten or more unique reach occurrences (e.g., Western Mosquitofish, Guppy, Common Molly, Green Swordtail, tilapia, Tahitian Prawn, Red Swamp Crayfish, American Bullfrog) using reach presence-absence dataset (see Chapter 3, Section 3.2.2 for a description). The species suitability models were built using a boosted regression tree (BRT) analysis (Elith et al. 2008). Boosted regression tree modeling is a machine learning method that has been increasingly utilized in ecological studies since introduced by Elith et al. (2008). Boosted regression tree models have the advantages of the tree-like models, including adapting both categorical and numerical variables as predictors, tolerating missing data, accommodating any type of prior distributions of data, incorporating interaction among predictors, and allowing for interpretation of nonlinear relationship with the resulting model. Most importantly, because of the boosting process of BRT, the predictive performance of BRT is greatly improved compared to traditional regression models.

4.2.2 Selection of model predictors

Models were developed using a combination of landscape scale predictors know to influence the distribution of stream fauna and significant landscape-scale variables identified via forward selection CCA. Four natural landscape factors (e.g., catchment area, slope, elevation, and groundwater contribution index) have been shown to affect fish assemblages (Marsh-Matthews & Matthews 2000) and to influence the distribution of fish species (Wang et al. 2003, Lyon et al. 2010). These variables, excluding groundwater contribution due to a lack of data availability, served as the initial predictors for building the models. Additional predictor variables were selected in a two-step process. A forward selection CCA was conducted with the selected taxa using reach presence-absence with a significance level ($p \leq 0.01$) and transformations identical to the forward selection CCA conducted in Chapter Three. The number of predictors identified in the forward selection CCA were reduced to avoid model overfitting. Overfitting describes when a model fits the calibration data too closely and fails to predict independent evaluation data accurately (Radosavljevic & Anderson 2014), this commonly occurs when a high number of predictor variables are used relative to data points. The number of predictors were reduced by only retaining variables with a p value less than or equal to 0.002 and explained variation greater than one percent.

4.2.3 Model development, evaluation, and prediction

Model development included a random ten-fold cross-validation that built the model with 90 percent of the data and utilizes the remaining 10 percent for validation. Models were built by varying the parameters tree complexity (tc) and learning rate (lr) until the number of trees (nt) included in the model exceeded 1000 (as suggested by Elith et al. 2008). Model learning rate controlled the contribution of each tree to the growing model, while tree complexity controled how interactions were fitted (Elith et al. 2008). A learning rate of 0.01 was initially implemented in model fitting and was subsequently halved to increase the number of trees, and a tree complexity of five was initially implemented in model fitting and subsequently reduced to three if necessary.

Model performance was evaluated by using the area under the curve method (AUC; Fielding & Bell 1997) to compare between model training, cross-validation, and predictive performance. The AUC was obtained by plotting the proportion of true positive against the proportion of false positive and by computing the areas under the curve (Fielding & Bell 1997). The AUC varies between zero and one, with zero representing a worse than random model, 0.5 representing a random model, and one representing the best model. The cross-validation AUC (CV AUC) was the primary statistic used to evaluated model performance, CV AUC scores greater than 0.90 represented good performance, CV AUC scores greater than 0.80 represented satisfactory performance, and CV AUC scores less than 0.80 represented poor performance.

The developed models of selected taxa were then applied to predict the suitability at each basic spatial unit (i.e. stream reach) with the predictor landscape variables throughout the five main Hawaiian Islands. The fixed 0.5 suitability (threshold) was used to determine the presence of the species at a given reach across the five main Hawaiian Islands. Predictions using the fixed 0.5 suitability were compared to the number of taxa reach observations used to develop the model. For each taxon with good or satisfactory performance, the predicted reach suitability was mapped using four probability classes (e.g., 0.000-0.250, 0.251-0.500, 0.501-0.750, 0.751-1.000), in conjunction with the observed occurrences used to build each model.

4.3. Results

4.3.1 Predictor selection

The forward selection CCA conducted with the selected taxa using reach presence-absence (eight taxa) indicated that the 24 significant (p value ≤ 0.01) environmental variables explained 34.0% of the total variation in taxa composition (Table 4.1). Among the 24 variables, nine variables were selected as model predictors based on criteria (p value = 0.002 and explained variation ≥ 1.0 %), listed in order of decreasing percent variation explained: downstream channel slope (D_Slope, 6.7%), upstream mean annual rainfall (U_MeanAnnRain, 3.5%), downstream road length density (D_RoadLen, 3.0%), local percent open water (L_OpWater, 2.5%), local mean air temperature (L_MeanTemp, 2.0%), downstream density of underground injection wells (D_UIC, 1.5%), upstream maximum annual rainfall (U_MaxAnnRain, 1.4%), local percent impervious surface (L_ImpSur, 1.2%), and downstream percent open water (D_OpWater, 1.1%). Note that, highly correlated variables to upstream mean annual rainfall and local mean air temperature were excluded from the landscape predictor selection. The final set of model predictors, including the three selected from the literature and nine selected from the forward selection CCA, were listed in Table 4.2 with the corresponding summary statistics including maximum, minimum, mean, and standard deviation.

4.3.2 Model parameters, evaluation statistics, and predictor contribution

Models were fit to the eight selected taxa (see Table 4.3 for a summary of model parameters and evaluation statistics including total and residual deviance). Taxa models with cross-validation AUC scores greater than 0.90 were Green Swordtail, Common Molly, and tilapia. Taxa models with cross-validation AUC scores greater than 0.80 were Western mosquitofish, Guppy, and Tahitian Prawn. The taxa American Bullfrog and Red Swamp Crayfish exhibited cross-validation AUC scores less than 0.80. American Bullfrog exhibited a score of 0.69 and Red Swamp Crayfish exhibited a score of 0.76. The relative contribution of predictor variables to taxon-specific models (Table 4.4) indicated that the importance of predictors generally varied among the taxa assessed. For taxa models with satisfactory (and good) performance, the most important predictors included channel slope (local and downstream), reach elevation, upstream mean annual rainfall, and local impervious surfaces. While the least important predictors among taxa included local open water and downstream UIC. Overall, the relative contributions of predictors indicated that those selected from literature sources preformed sufficiently compared to the predictors selected from the forward selection CCA.

4.3.4 Taxa predictions

Species suitability models were built upon the species-environment associations, see Table 4.5 for a summary of taxa observations, predicted presence reaches via fixed 0.5, and the respective distribution among stream hydrological classes. For taxa with good and satisfactory model performance (e.g., Green Swordtail, Common Molly, and tilapia, Western mosquitofish, Guppy, and Tahitian Prawn), as designated by CV AUC scores, the predicted number of presence reaches were greater than the number of reaches where the taxa were observed to occur. This suggested the distribution of the species could be wider than the observations from survey records. Except for Common Molly, for which the number of predicted presence reaches was less than the number of observed reach occurrences used to build the model, which suggested additional biological surveys were needed to better understand the species-environment association.

The spatial distributions of predicted reach suitability indicated that the poeciliid fishes (e.g., Western Mosquitofish, Green Swordtail, and Guppy; Figure 4.1, 4.2, and 4.3 respectively) exhibited similar areas with high probability of reach suitability, including windward Kauaʻi, central Oʻahu, and one stream in central Maui. While tilapia suitability prediction (Figure 4.5) identified prominent areas such as the lower-elevation coastal reaches on windward Kauaʻi, most of Oʻahu, and central Maui. Tahitian Prawn suitability prediction (Figure 4.5) was the most prevalent of all taxa assessed, and included north and south Kauaʻi, central and windward Oʻahu, and the windward areas of Molokaʻi, Maui, and Hawaiʻi Island.

4.4 Discussion

This chapter modeled the potential distribution of introduced stream taxa via reach suitability throughout the five main Hawaiian Islands. Satisfactory models were developed for five of the eight taxa assessed. Among these taxa, poeciliid fishes at the species level (e.g., Western Mosquitofish, Green Swordtail, and Guppy) exhibited similar spatial distributions of suitability predictions with minor differences among species. While tilapia and Tahitian Prawn exhibited markedly unique suitability distributions predictions compared to each other and the poeciliid fishes. Of these taxa, Tahitian Prawn exhibited the greatest number of suitable reaches, followed next by Western Mosquitofish, and lastly by Green Swordtail. Areas with the greatest suitability among taxa included the low-sloped and low-elevation areas of Oʻahu, windward Kauaʻi, and central Maui, as well as select streams on Molokaʻi and Hawaiʻi Island.

When modeling the habitat suitability of introduced species within their non-native range, the species-environmental association applied to build the model could be established based within its native range (e.g., Ficetola et al. 2007) or based within the non-native range (e.g., Britton et al. 2010). The use of these two modeling strategies often reflect differences in data availability, spatial scale, and ecological motivations. The use of species-environmental associations based within the non-native range has advantages such as incorporating novel environments and biotic interactions that were not part of the association within their native range and that may influence species habitat suitability or distributions at the non-native environment of interest (Jiménez-Valverde et al. 2011). However, the comprehensiveness of modeling introduced species based on their non-native range can be questioned due to the modeling assumption of species equilibrium (Gallien et al. 2012). The species equilibrium concept assumes that the species have already reached all suitable locations and are absent from all unsuitable locations (Guisan & Thuiller 2005). Depending on the species, modeling introduced stream species in Hawaiʻi likely violates this assumption, as it is possible that introduced species have not been introduced to all watersheds. Some exceptions may include introduced stream species that have exhibited means of natural dispersal between watersheds (e.g., Tahitian Prawn via amphidromous lifecycle, Blackchin Tilapia via high salinity tolerance, and American Bullfrog via terrestrial movement; Brown et al. 1999, Englund et al. 2000, Gahl et al. 2009). However, there is insufficient evidence to suggest that these species have reached equilibrium in Hawaiʻi.

The development of taxa suitability models in this study were based on the observations of taxa throughout Hawaiʻi, i.e., the non-native range of the taxa. This strategy was adopted with the consideration of the unique characteristics of Hawaiian streams, including small size, large changes in elevation, and flashy streamflow. All of these factors likely presented unique obstacles for introduced species and influenced species-environmental factor associations that were not represented in their native ranges. Our model development results also showed that minimum elevation, downstream slope, and upstream mean rainfall were important predictors of many species, which further validated the choice of this strategy, as these factors might not show association with species in their native range. For example, in Chapter Three Western Mosquitofish was associated with a larger range of stream channel slopes in Hawaiʻi as compared to the species native range (e.g., Southern United States).

The poeciliid fish species (e.g., Western Mosquitofish, Green Swordtail, and Guppy) exhibited similar trends in the distributions of suitable reaches. Of these three taxa, Western Mosquitofish exhibited the greatest number of suitable reaches outside of its observed occurrences, which indicated the greatest potential to expand its current range. However, the majority of these reaches were intermittent reaches, and are generally less important when considering the conservation of native stream species compared to perennial reaches. With respect to perennial reaches, Western Mosquitofish and Green Swordtail exhibited a greater number of suitable reaches as compared to Guppy, and thus may pose more of a threat to native stream species.

The predicted suitability for tilapia was primarily restricted to the lower coastal reaches of streams, specifically those with low-sloped urban areas with low upstream rainfall. The tilapia prediction corresponded with the documented occurrence of these species (e.g., Blackchin Tilapia) in coastal stream reaches that have mixtures of salt and freshwater (i.e., tidally influenced estuarine areas; Englund et al. 2000). The reach suitability of tilapia may be driven by the natural weathering of islands, as older islands typically have more eroded stream channels that are often characterized by larger streams, more meanders, mild slopes, which cumulatively result in prevalent estuarine areas in the lower stream reaches. Whereas, younger islands typically have less eroded streams channels, which often have steep stream slopes near the coast resulting in a lack of estuarine areas in coastal areas. Human development likely served as a secondary driver of tilapia reach suitability, as many coastal developments such as breakwaters, harbors, flood control structures, and road crossings result in larger areas with brackish conditions in lower streams that are subject to warmer temperatures and decreased wave action.

Of the taxa modeled, Tahitian Prawn prediction exhibited the largest amount of suitable reaches, with drastically different patterns compared to other taxa models. The suitable reaches of the prawn generally included the windward streams of all islands. Given the ability of the Tahitian Prawn to naturally disperse to new streams via its amphidromous life history (Fitzsimons et al. 2007), this suitability prediction may be more representative of the actual distribution of this species. The largely windward-based suitability corresponds with approximately two-thirds of the predicted suitable reaches classified as perennial streams. This is concerning from a management perspective given that perennial streams are considered the most important habitats for native stream species (Yamamoto & Tagawa 2000). Future investigation is needed to understand if Tahitian Prawn is competing habitat resources with Hawaiian native stream species or as one of the predators to the native species.

Overall, the models indicated that reach suitability for introduced species was largely influenced by factors operating across islands as well as between islands. Across the islands, elevation appeared to be the dominant factor influencing reach suitability. While the predicted suitability varied among taxa with regards to elevation, the suitable reaches for all taxa were generally limited to lower elevations. Between islands, a combination of stream channel slope, largely reflected by island age, and human influences were the dominant factors influencing reach suitability. These two factors were interrelated as human influences, including urbanization and agriculture, are generally most concentrated in low-sloped areas. Given the ecological variation among the modeled taxa, these low-elevation, low-sloped, reaches prone to human activities were likely strong indicators of reach suitability for many of the introduced species found throughout Hawaiʻi. Areas in Hawaiʻi that exhibit these characteristics suitable to introduced stream species include the lower reaches of windward Kauaʻi, central and windward areas of Oʻahu, and a few streams across Molokaʻi, Maui, and Hawaiʻi Island.

The prediction of low-elevation reaches being suitable for introduced species in Hawai'i agreed with the findings of Brasher et al. (2006), which indicated that elevation and urbanization were the dominant drivers of introduced species throughout Hawaiʻi. The finding of the importance of channel slope in this study compared to urbanization in Brasher et al. (2006) likely represents differences in methodology, as this study was modeling suitable areas while Brasher et al. (2006) was investigating species occurrences in field surveys. Therefore, low-sloped reaches were likely suitable for introduced species, while urbanized areas (which occur primarily in low-sloped areas) resulted in an increased number of human-mediated species introductions to these suitable areas. This has resulted in urbanized low-sloped areas becoming inhabited by introduced species before less-inhabited low-sloped areas. This phenomenon was likely amplified due to the additional habitat alterations that are associated with urbanization, which likely promote the success of introduced species.

Of the taxa with unsatisfactory models, including Common Molly, Red Swamp Crayfish, and American Bullfrog, the failure to adequately model the suitable reaches was likely due to a combination of low number of observations and a failure to include important landscape predictors. The failure to model Common Molly was primarily attributed to low number of observational values (e.g., 11 reaches).The failure to successfully model Red Swamp Crayfish and American Bullfrog could be primarily attributed to a lack of including important landscape predictors, potentially those representing still or slow-moving stream environments. While both species have been documented to occur in stream habitats, they have commonly utilized still or slow-moving waters such as lakes, ponds, swamps, and marshes (Graves & Anderson 1987, Huner & Barr 1991). Therefore, landscape predictors that may capture these types of environments may include stream proximity to landscape features such as marshes, taro fields, lakes, and small ponds that occur on golf courses, farming areas, and residential areas. Additionally, the overgrowth of hau bush (*Hibiscus tiliaceus*) into stream channels may be an important factor as it has been documented to create “swamp-like” conditions in Hawaiian streams by slowing water and holding organic matter (Fitzsimons et al. 2005).

4.5 Conclusion

This modeling assessment demonstrated that there were similarities and differences among the distribution of suitable reaches of introduced species in Hawaiʻi. Generally, suitable reaches for all taxa were predicted in low elevation and low slope areas, and especially those with dense human populations. These suitable reaches were concentrated on the islands of Oʻahu and Kauaʻi, possibly reflecting the more-developed erosional processes in the stream geomorphology that occur with island age. Among taxa, differences in reach suitability appeared to be influenced by taxon-specific responses to elevation, slope, and rainfall. Tilapia was primarily predicted at coastal reaches in urbanized areas, the three poecilids (e.g., Western Mosquitofish, Green Swordtail, and Guppy) spanned a larger range of elevations, slopes, and rainfalls, with minor differences between species, and the Tahitian Prawn exhibited the most unique prediction which entailed the windward sides of all islands, including areas with increased rainfall and channel slopes. Of the taxa assessed, Tahatian Prawn exhibited the largest potential distribution, as well as the greatest overlap with native species. This modeling exercise identified stream reaches that exhibited potential to support introduced species. Additional surveys could be considered to detect their presence or absence at those identified areas and to design control management and strategies.

Chapter Four Tables

Table 4.1. Forward selection canonical correspondence analysis results of selected taxa composition with significant (*p* value ≤ 0.01) landscape factors using reach presence-absence. (*) indicated the factors that were kept among all the correlated landscape factors.

Summary: Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4147	0.2096	0.1452	0.103
Explained variation (cumulative)	12.96	19.50	24.04	27.26
Pseudo-canonical correlation	0.7957	0.6268	0.6000	0.4724
Explained fitted variation (cumulative)	38.16	57.45	70.81	80.29

Forward Selection Results: Name	Explains %	Contribution %	pseudo-F	P
D_Slope	6.7	12.3	24.4	0.002
U_MeanAnnRain*	3.5	6.4	13.2	0.002
D_RoadLen	3.0	5.6	11.8	0.002
L_OpWater	2.5	4.6	10.0	0.002
L_MeanTemp*	2.0	3.7	8.2	0.002
D_UIC	1.5	2.8	6.3	0.002
U_MaxAnnRain	1.4	2.6	5.9	0.002
L_ImpSur	1.2	2.2	5.2	0.002
D_OpWater	1.1	2.0	4.6	0.002
L_UncShr	1.1	2.1	4.9	0.004
L_DitchLen	1.0	1.9	4.6	0.004
D_EsWet	0.9	1.7	4.1	0.004
U_CERCLIS*	0.9	1.7	4.0	0.006
U_MinSoilPerm	0.7	1.4	3.3	0.004
U_OpWater	0.7	1.4	3.4	0.008
U_Dam	0.7	1.4	3.4	0.002
D_Forest	0.7	1.4	3.4	0.002
U_PipeLen	0.6	1.1	2.8	0.008
U_OpDev	0.6	1.1	2.9	0.01
U_FormPlan	0.7	1.2	3.2	0.01
D_DitchX	0.6	1.1	2.8	0.01
U_ImpSur	0.6	1.1	2.9	0.006
L_OpDev	0.6	1.2	3.1	0.006
U_303D	0.5	1.0	2.6	0.008

Table 4.2. Predictor variables selected for taxa habitat suitability models, and summary statistics of the variables used to build the models including mean, minimum-maximum (Min-Max), and standard deviation (SD). (*) indicates the variable was selected based on literature sources (Marsh-Matthews & Matthews 2000), other variables were selected from forward selection CCA.

Code	Variable	Units	Mean	Min-Max	SD
D_OpWater	Downstream percent open water	%	1.78	0-35.00	3.25
D_RoadLen	Downstream road length density	km/km^2	3.45	0-58.23	4.11
D_Slope	Downstream main channel slope	%	7.47	0.0082-85.15	7.64
D_UIC	Downstream density of underground injection wells	#/km^2	0.03	0-2.03	0.15
L_ImpSur	Local percent impervious surfaces	%	3.38	0-79.90	8.53
L_MeanTemp	Local mean annual air temperature	°C	21.93	16.90-24.55	1.53
L_MinEle*	Minimum reach elevation	m	147.39	0-729.00	155.36
L_OpWater	Local percent open water	%	1.84	0-41.38	4.81
L_Slope*	Local reach slope	%	10.37	0-87.15	11.89
U_Area*	Upstream catchment area	km^2	18.00	0.13-395.22	43.28
U_MaxAnnRain	Upstream maximum annual rainfall	mm/yr	4888.41	1042.27-9989.51	2057.94
U_MeanAnnRain	Upstream mean annual rainfall	mm/yr	3553.41	755.52-7225.82	1395.00

Table 4.3. Model parameters and evaluation statistics for the selected taxa. Tree complexity (tc) and learning rate (lr) are model parameters that respectively control how interactions are fitted and the contribution of each tree to the growing model. Number of trees (nt) indicates the number of trees implemented for optimal prediction. Mean total deviance (Mean Total Dev.), mean residual deviance (Mean Resid. Dev.), estimated cross validation deviance (Est. CV Dev.), and estimated cross validation standard error (Est. CV SE) described the variation observed in each model and cross validation. Training AUC (area under the curve), cross validation AUC (CV AUC), and cross validation AUC standard error (CV AUC SE) are parameters used to evaluate model accuracy. WM = Western Mosquitofish, GS = Green Swordtail, GU = Guppy, CM = Common Molly, TI = tilapia, AB = American Bullfrog, TP = Tahitian Prawn, and RS = Red Swamp Crayfish.

Taxa	**tc**	**lr**	**nt**	**Mean Total Dev.**	**Mean Resid. Dev.**	**Est. CV Dev.**	**Est. CV SE**	**Training AUC**	**CV AUC**	**CV AUC SE**
WM	5	0.00125	2200	0.66	0.32	0.52	0.03	0.97	0.85	0.03
GS	5	0.00125	4500	0.80	0.25	0.54	0.04	0.99	0.90	0.01
GU	5	0.00125	3250	0.74	0.30	0.55	0.02	0.98	0.86	0.02
CM	3	0.00125	1400	0.17	0.06	0.13	0.01	1.00	0.94	0.01
TI	3	0.0025	1200	0.35	0.09	0.19	0.03	0.99	0.94	0.03
AB	5	0.000625	1900	0.34	0.21	0.32	0.02	0.98	0.69	0.06
TP	5	0.0025	2850	1.33	0.60	0.98	0.03	0.97	0.83	0.01
RS	3	0.00125	1750	0.28	0.14	0.25	0.01	0.99	0.76	0.05

Table 4.4. Relative contribution of predictor variables to taxa models with values of the top three most important predictors bolded for each taxon. Model predictors are downstream percent open water (D_OpWater), downstream road length density (D_RoadLen), downstream channel slope (D_Slope), downstream underground injection well density (D_UIC), local percent impervious surfaces (L_ImpSur), local mean air temperature (L_MeanTemp), local percent open water (L_OpWater), local channel slope (L_Slope), upstream catchment area (U_Area), upstream maximum annual rainfall (U_MaxAnnRain), and upstream mean annual rainfall (U_MeanAnnRain). Taxa codes are WM = Western Mosquitofish, GS = Green Swordtail, GU = Guppy, CM = Common Molly, TI = tilapia, AB = American Bullfrog, TP = Tahitian Prawn, and RS = Red Swamp Crayfish.

Taxa	**D_Op Water**	**D_Road Len**	**D_Slope**	**D_UIC**	**L_Imp Sur**	**L_Mean Temp**	**L_Min Ele**	**L_Op Water**	**L_Slope**	**U_Area**	**U_Max AnnRain**	**U_Mean AnnRain**
WM	8.53	5.27	9.35	**13.45**	5.33	8.92	5.98	2.89	**12.74**	8.92	7.34	**11.29**
GS	6.99	**10.02**	**22.19**	2.55	**9.98**	8.03	4.66	7.81	6.08	7.84	5.56	8.28
GU	7.74	6.73	10.01	5.28	**12.86**	6.99	5.39	8.72	**10.50**	**10.69**	7.21	7.89
CM	8.71	2.30	**22.17**	0.00	3.67	**19.98**	10.19	2.40	**14.43**	2.01	8.11	6.03
TI	1.00	2.36	**28.68**	0.41	**24.72**	3.25	10.24	2.38	6.26	3.52	4.48	**12.70**
AB	9.71	6.34	5.46	1.23	5.79	10.28	**19.89**	2.17	**16.51**	6.81	5.45	**10.36**
TP	6.64	6.89	6.72	1.57	5.71	9.19	**19.18**	8.19	5.47	8.50	**12.10**	**9.84**
RS	10.84	**15.02**	7.32	2.63	9.95	**12.08**	9.95	4.97	4.22	5.57	**13.26**	4.18

Table 4.5. Predicted number of suitable reaches within the five main Hawaiian Islands for taxa models, using fixed 0.5 to indicate suitable reaches. Observed indicated the number of taxon reach occurrences used the build the respective model. For each group, total indicates the total number of reaches, while perennial (Per.), intermittent (Int.), and not classified (NC) indicate the distribution of reaches among hydrograph classifications. WM = Western Mosquitofish, GS = Green Swordtail, GU = Guppy, CM = Common Molly, TI = tilapia, AB = American Bullfrog, TP = Tahitian Prawn, and RS = Red Swamp Crayfish.

Taxa	**Observed**				**Predicted (fixed 0.5)**			
	Total	**Per.**	**Int.**	**NC**	**Total**	**Per.**	**Int.**	**NC**
WM	65	56	7	2	576	133	378	65
GS	87	70	12	5	314	149	146	19
GU	77	59	13	5	181	84	85	12
CM	11	10	0	1	4	2	0	2
TI	27	15	6	6	259	77	64	118
AB	26	20	4	2	0	0	0	0
TP	246	194	42	10	1165	691	394	80
RS	20	17	3	0	14	3	10	1

Chapter Four Figures

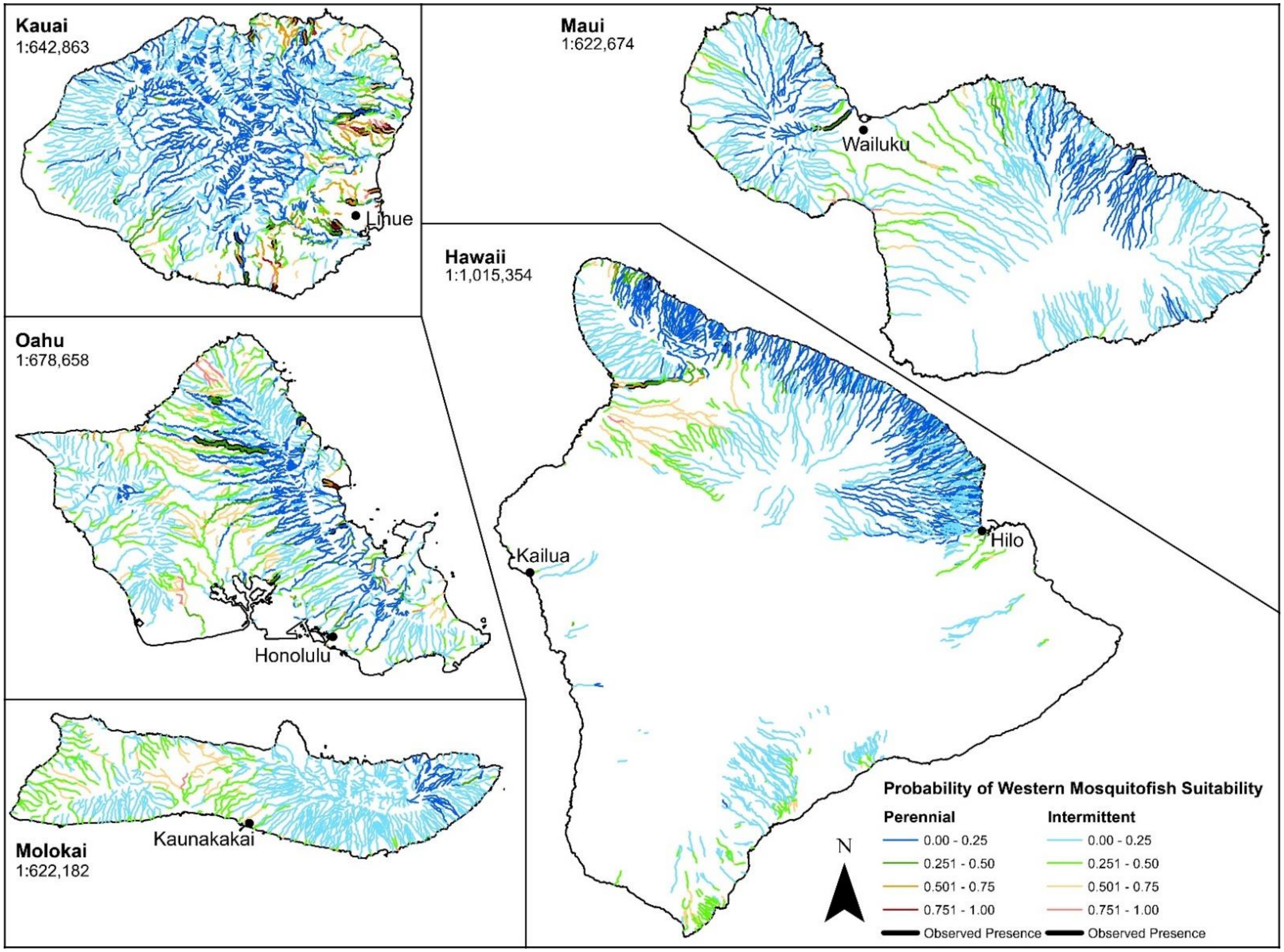


Figure 4.1. Modeled reach suitability for Western Mosquitofish. Probability of reach suitability was designated by color with blue (0.000 – 0.250), green (0.251 – 0.500), orange (0.501 – 0.750), red (0.751 – 1.000), darker color shades indicate perennial streams, lighter shades indicate intermittent or non-classified streams. Reaches with observed taxa presence were outlined in black.

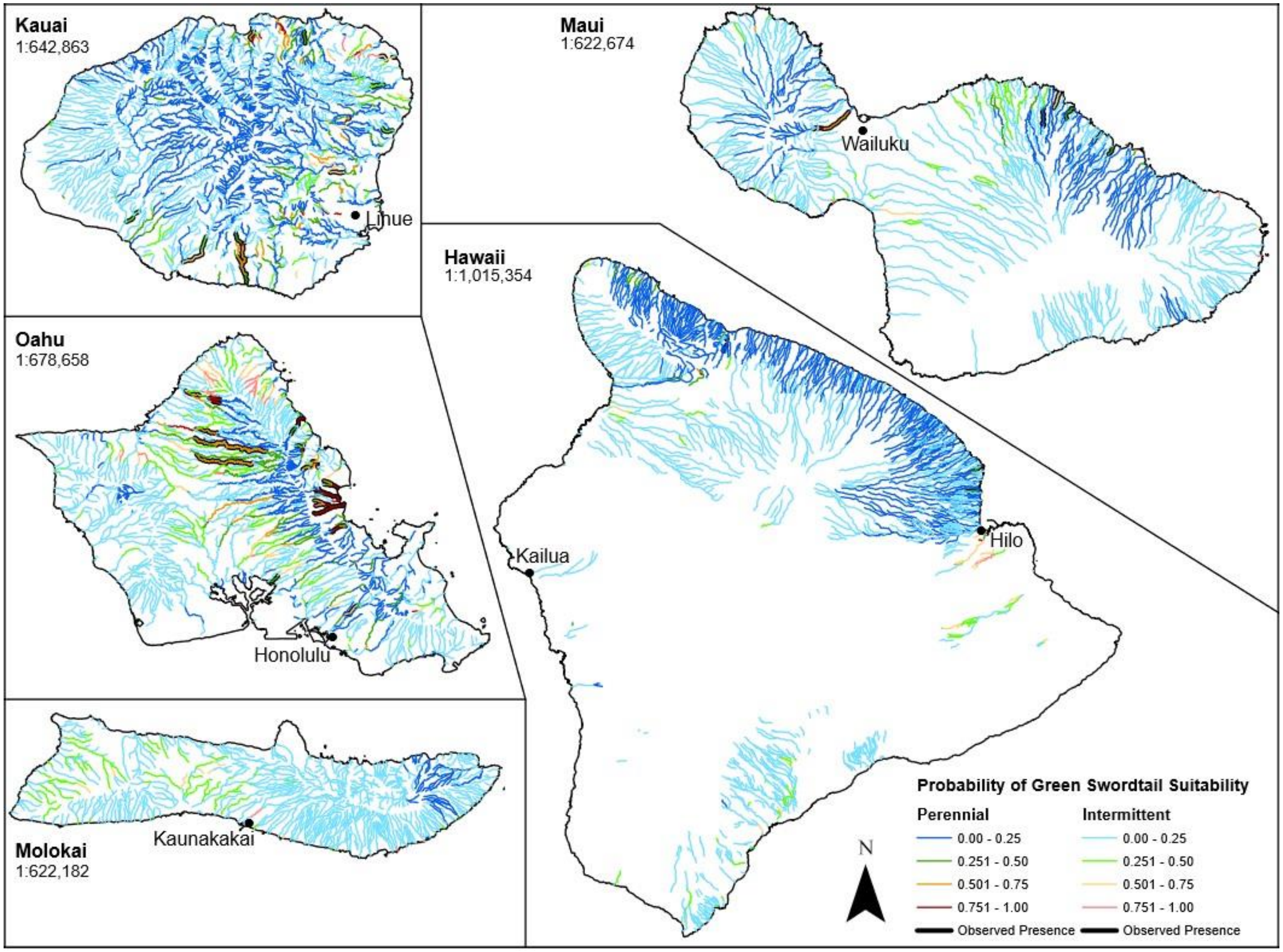


Figure 4.2. Modeled reach suitability for Green Swordtail. Probability of reach suitability was designated by color with blue (0.000 – 0.250), green (0.251 – 0.500), orange (0.501 – 0.750), red (0.751 – 1.000), darker color shades indicate perennial streams, lighter shades indicate intermittent or non-classified streams. Reaches with observed taxa presence were outlined in black.

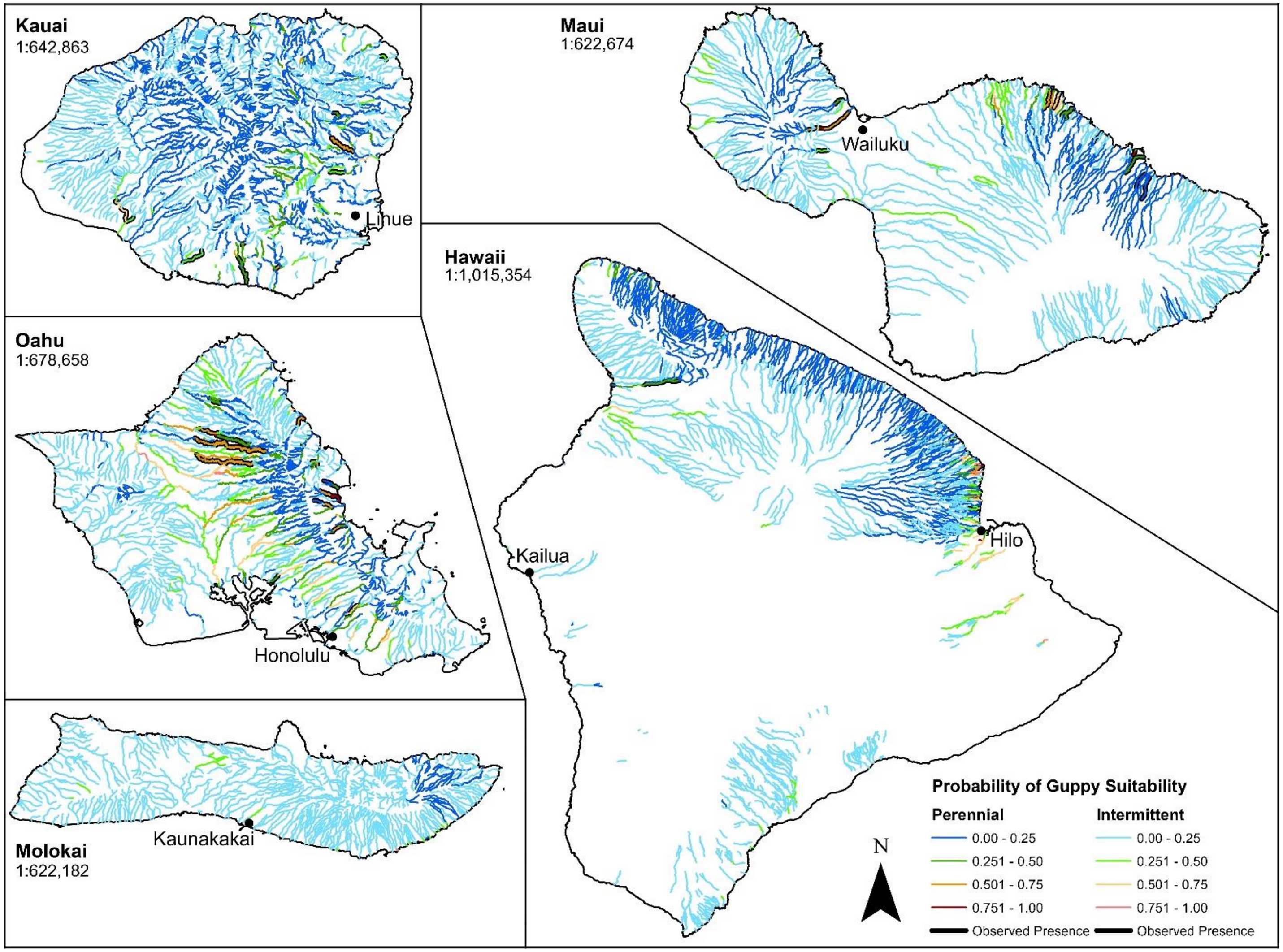


Figure 4.3. Modeled reach suitability for Guppy. Probability of reach suitability was designated by color with blue (0.000 – 0.250), green (0.251 – 0.500), orange (0.501 – 0.750), red (0.751 – 1.000), darker color shades indicate perennial streams, lighter shades indicate intermittent or non-classified streams. Reaches with observed taxa presence were outlined in black.

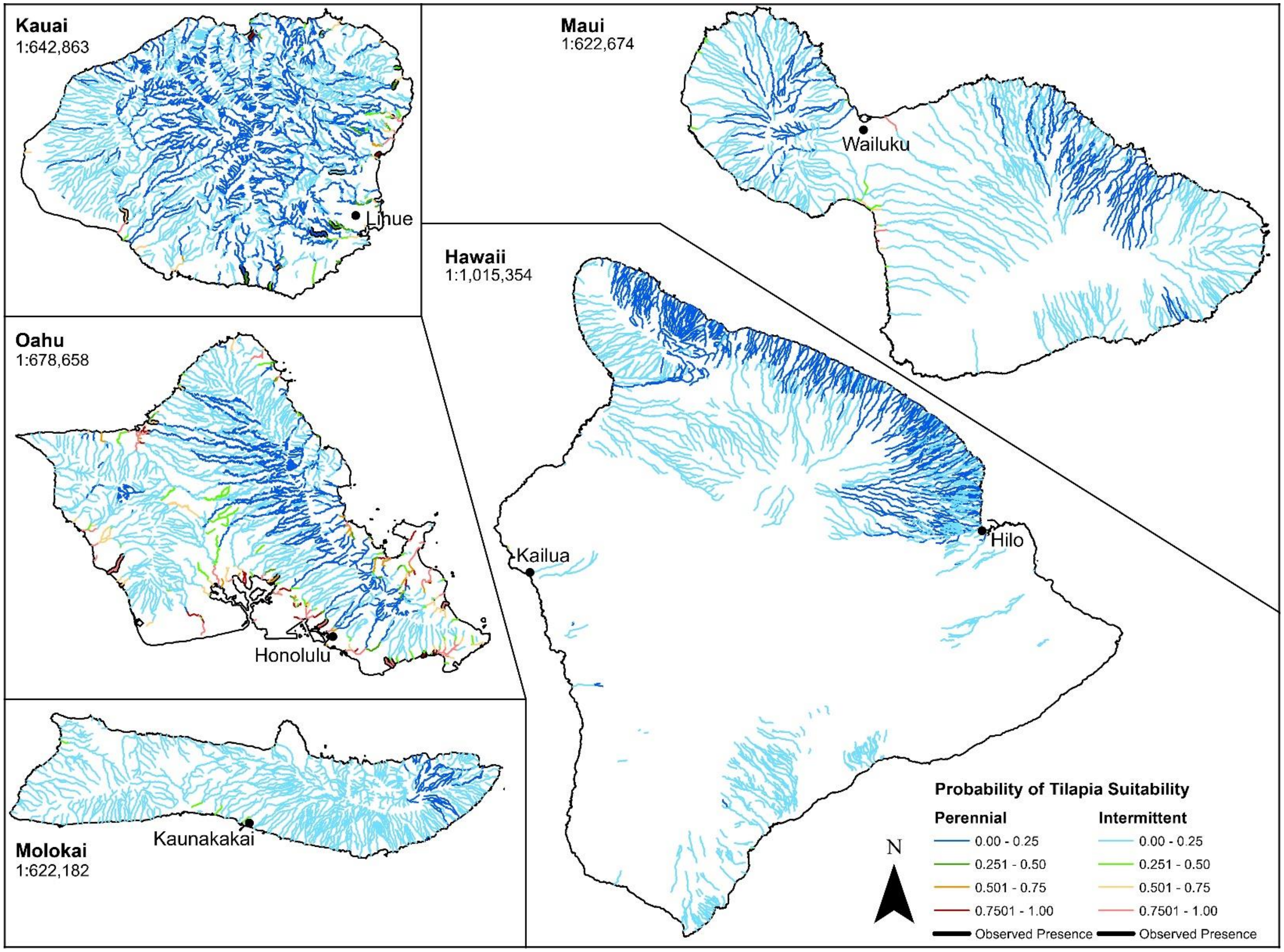


Figure 4.4. Modeled reach suitability for tilapia. Probability of reach suitability was designated by color with blue (0.000 – 0.250), green (0.251 – 0.500), orange (0.501 – 0.750), red (0.751 – 1.000), darker color shades indicate perennial streams, lighter shades indicate intermittent or non-classified streams. Reaches with observed taxa presence were outlined in black.

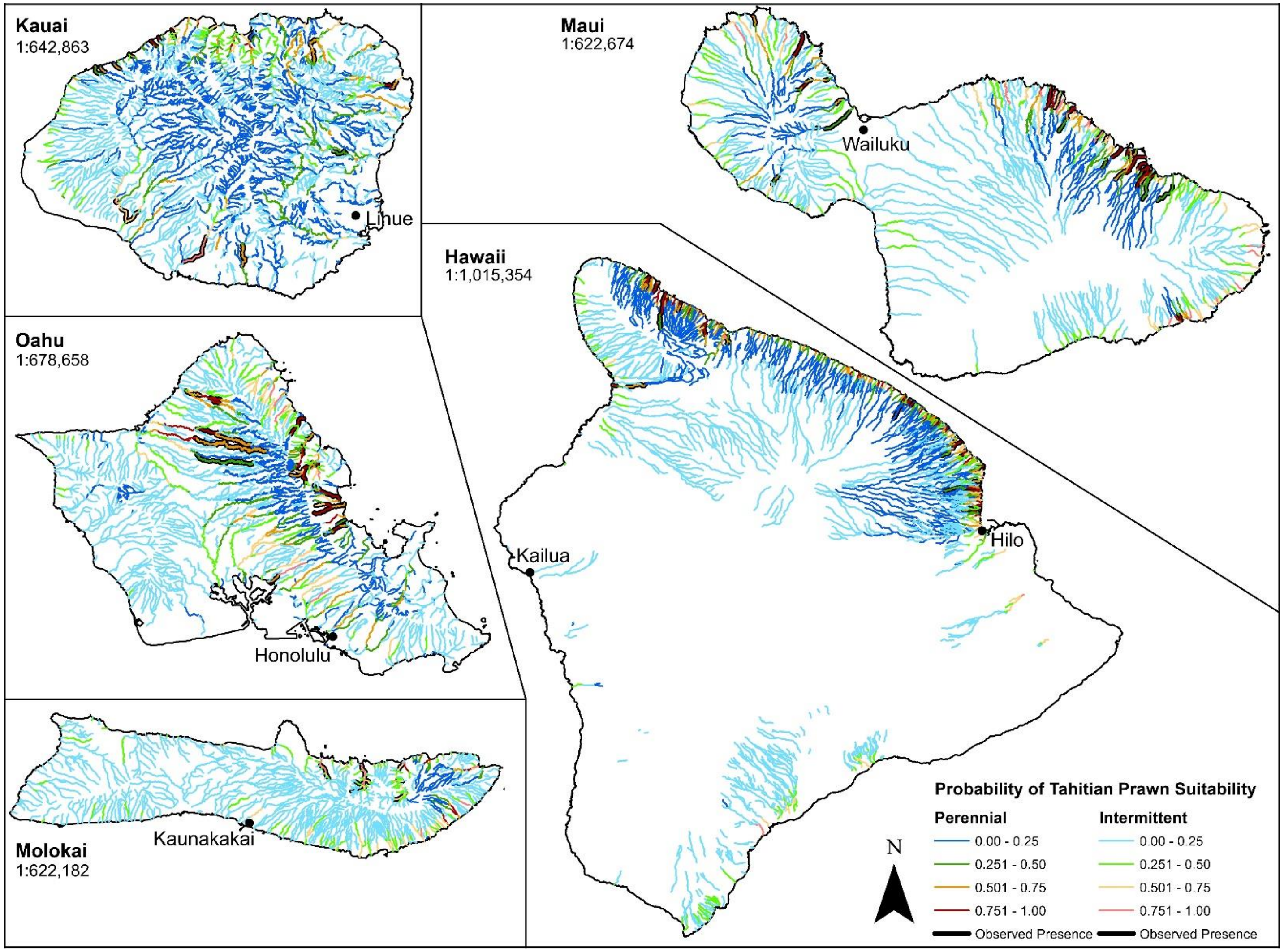


Figure 4.5. Modeled reach suitability for Tahitian Prawn. Probability of reach suitability was designated by color with blue (0.000 – 0.250), green (0.251 – 0.500), orange (0.501 – 0.750), red (0.751 – 1.000), darker color shades indicate perennial streams, lighter shades indicate intermittent or non-classified streams. Reaches with observed taxa presence were outlined in black

References

Allan, J. D. (2004). Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology Evolution and Systematics, 35, 257-284.

Allan, J. D., Erickson, D., & Fay, J. (1997). The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology, 37, 149-161.

Arthington, A. H., Blüdhorn, D. R., & Kennard, M. J. (1994). Food resource partitioning by the introduced cichlid, *Oreochromis mossambicus*, and two native fishes in a subtropical Australian impoundment. Third Asian Fisheries Forum, 425-428.

Baker, M. E., & King, R. S. (2010). A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods in Ecology and Evolution, 1, 25-37.

Baker, M. E., King, R. S., & Kahle, D. (2015). TITAN2: Threshold Indicator Taxa Analysis. R package version 2.1. https://CRAN.R-project.org/package=TITAN2.

Bhaskar, M., & Govindappa, S. (1986). Effect of environmental acidity and alkalinity on the physiology of *Tilapia mossambica* during acclimation. Biochemical Systematics and Ecology, 14, 439-443.

Blumenstock, D.I., & Price, S. (1967). Climate of Hawaii, in Climates of the States, no. 60-51, Climatography of the United States: U.S. Department of Commerce.

Bowen, S. H. (1982). Feeding, digestion and growth-qualitative considerations. The Biology and Culture of Tilapias, 7, 141-156.

Brasher, A. M. (2003). Impacts of human disturbances on biotic communities in Hawaiian streams. BioScience, 53, 1052-1060.

Brasher, A. M., Luton, C. D., Goodbred, S. L., & Wolff, R. H. (2006). Invasion patterns along elevation and urbanization gradients in Hawaiian streams. Transactions of the American Fisheries Society, 135, 1109-1129.

Britton, J. R., Cucherousset, J., Davies, G. D., Godard, M. J., & Copp, G. H. (2010). Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. Freshwater Biology, 55, 1130-1141.

Brock, V. E. (1960). The introduction of aquatic animals into Hawaiian waters. Internationale Revue der gesamten Hydrobiologie, 45, 463-480.

Brown, L. R., Brasher, A. M., Harvey, B. C., & Matthews, M. (1999). Success and failure of nonindigenous aquatic species in stream systems: Case studies from California and Hawaii. Nonindigenous Freshwater Organisms: Vectors, Biology, and Impacts. Boca Raton (FL): Lewis Publishers, 415-430.

Buisson, L., Blanc, L., & Grenouillet, G. (2008). Modelling stream fish species distribution in a river network: the relative effects of temperature versus physical factors. Ecology of Freshwater Fish, 17, 244-257.

Bury, R. B., & Whelan, J. A. (1984). Ecology and management of the bullfrog. U.S. Fish and Wildlife Service, Resource Publication 155.

Carmona-Catot, G., Benito, J., & García-Berthou, E. (2011). Comparing latitudinal and upstream–downstream gradients: life history traits of invasive mosquitofish. Diversity and Distributions, 17, 214-224.

Cheek, B. D., Grabowski, T. B., Bean, P. T., Groeschel, J. R., & Magnelia, S. J. (2016). Evaluating habitat associations of a fish assemblage at multiple spatial scales in a minimally disturbed stream using low-cost remote sensing. Aquatic Conservation: Marine and Freshwater Ecosystems, 26, 20-34.

Cooper, A. R., Infante, D. M., Wehrly, K. E., Wang, L., & Brenden, T. O. (2016). Identifying indicators and quantifying large-scale effects of dams on fishes. Ecological Indicators, 61, 646-657.

Cooper, J. A. G., & Harrison, T. D. (1992). Effects of nesting activities of *Oreochromis mossambicus* (Pisces: Cichlidae) on bank stability in small lagoons. South African Journal of Science, 88, 398-401.

Crawford, S., Whelan, G., Infante, D.M., Blackhart, K., Daniel, W.M., Fuller, P.L., Birdsong, T., Wieferich, D.J., McClees-Funinan, R., Stedman, S.M. & Herreman, K. (2016). Through a fish's eye: the status of fish habitat in the United States 2015. National Fish Habitat Partnership, Washington, DC. Available: assessment. fishhabitat.org.

Daniel, W.M., Infante, D.M., Hughes, R.M., Tsang, Y.P., Esselman, P.C., Wieferich, D., Herreman, K., Cooper, A.R., Wang, L. & Taylor, W.W. (2015). Characterizing coal and mineral mines as a regional source of stress to stream fish assemblages. Ecological Indicators, 50, 50-61.

Dauwalter, D. C., Splinter, D. K., Fisher, W. L., & Marston, R. A. (2008). Biogeography, ecoregions, and geomorphology affect fish species composition in streams of eastern Oklahoma, USA. Environmental Biology of Fishes, 82, 237-249.

Devaney, D. M., Kelly, M., Lee, P. J., & Motteler, L. S. (1982). Kãneʻohe, a history of change. Bess Pr Inc.

Devick, W. S. (1991). Patterns of introductions of aquatic organisms to Hawaiian freshwater habitats. New Directions in Research, Management, and Conservation of Hawaiian Freshwater Stream Ecosystems: Proceedings of the 1990 Symposium on Stream Biology and Fisheries Management, State of Hawaii, Dept. of Land and Natural Resources, Division of Aquatic Resources, Honolulu.

Drake, J.M. & Bossenbroek, J.M. (2004) The potential distribution of zebra mussels in the United States. BioScience, 54, 931–941.

Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological monographs, 67, 345-366.

Eldredge, L. G. (1992). Unwanted strangers: An overview of animals introduced to Pacific Islands. Pacific Science, 46, 384-386.

Eldredge, L. G., & Humphries, J. D. (1994). Perspectives in aquatic exotic species management in the Pacific Islands: Volume I, Introductions of commercially significant aquatic organisms to the Pacific Islands. South Pacific Commission, Noumea, New Caledonia.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. Journal of Animal Ecology, 77, 802-813.

Endler, J. A. (1995). Multiple-trait coevolution and environmental gradients in guppies. Trends in ecology & evolution, 10, 22-29.

Englund, R. E. (1999). The impacts of introduced poeciliid fish and Odonata on the endemic Megalagrion (Odonata) damselflies of Oahu Island, Hawaii. Journal of Insect Conservation, 3, 225-243.

Englund, R. A., Arakaki, K., Preston, D.J., Coles, S.L., & Eldredge, L.G. (2000a). Nonindigenous freshwater and estuarine species introductions and their potential to affect sportfishing in the lower stream and estuarine regions of the south and west shores of Oahu, Hawaii: final report prepared for the Hawaii Department of Land and Natural Resources, Division of Aquatic Resources (No. 17). Bishop Museum Press.

Englund, R. A., Preston, D. J., Wolff, R., Coles, S.L., Eldredge, L.G., & Arakaki, K. (2000b). Biodiversity of freshwater and estuarine communities in lower Pearl Harbor, Oahu, Hawaii with observations on introduced species: final report prepared for the US Navy (No. 16). Bishop Museum Press.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes: A Continuous View of the River is Needed to Understand How Processes Interacting among Scales Set the Context for Stream Fishes and Their Habitat. BioScience, 52, 483-498.

Ficetola, G. F., Thuiller, W., & Miaud, C. (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. Diversity and Distributions, 13, 476-485.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental conservation, 24, 38-49.

Fitzsimons, J. M., McRae, M. G., & Nishimoto, R. T. (2007). Behavioral ecology of indigenous stream fishes in Hawai'i. Evenhuis, N.L. & Fitzsimons, J.M. (Eds.), Biology of Hawaiian Streams and Estuaries (11-21). Bishop Museum Bulletin in Cultural and Environmental Studies.

Fitzsimons, J. M., Parham, J. E., Benson, L. K., McRae, M. G., & Nishimoto, R. T. (2005). Biological assessment of Kahana Stream, Island of O 'ahu, Hawai 'i: An application of PABITRA survey methods. Pacific Science, 59, 273-281.

Fitzsimons, J.M., Schoenfuss, H.L., & Schoenfuss, T.C. (1997). Significance of Unimpeded Flows in Limiting the Transmission of Parasites from Exotics to Hawaiian Stream Fishes. Micronesia, 30, 117-125.

Font, W. F., & Tate, D. C. (1994). Helminth parasites of native Hawaiian freshwater fishes: an example of extreme ecological isolation. The Journal of parasitology, 682-688.

Fortini, L., Price, J., Jacobi, J., Vorsino, A., Burgett, J., Brinck, K., Amidon, F., Miller, S., Gon III, S., Koob, G. & Paxton, E., (2013). A landscape-based assessment of climate change vulnerability for all native Hawaiian plants (No. TR HCSU-044). University of Hawaii.

Frissell, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental management, 10, 199-214.

Froese, R., & Pauly, D. (2017). FishBase; 2017. World Wide Web electronic publication. Available at: http://www.fishbase.org.

Gahl, M. K., Calhoun, A. J., & Graves, R. (2009). Facultative use of seasonal pools by American bullfrogs (Rana catesbeiana). Wetlands, 29, 697-703.

Giambelluca, T.W., Nullet, M.A., & Schroeder, T.A. (1986). Rainfall atlas of Hawaii: State of Hawaii, Department of Land and Natural Resources, Division of Water and Land Development, Report R76.

Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, Y.L., Chu, P.S., Eischeid, J.K. & Delparte, D.M. (2013). Online rainfall atlas of Hawaiʻi. Bulletin of the American Meteorological Society, 94, 313-316.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models–how violating the equilibrium assumption can create new insights. Global Ecology and Biogeography, 21, 1126-1136.

Google Inc. (2017). Google Earth Pro: Version 7.3.0.3832. Mountain View, CA.

Govindarajulu, P., Price, W. M. S., & Anholt, B. R. (2006). Introduced bullfrogs (*Rana catesbeiana*) in western Canada: has their ecology diverged?. Journal of Herpetology, 40, 249-260.

Graves, B. M., & Anderson, S. H. (1987). Habitat suitability index models: bullfrog (No. 82/10.138). US Fish and Wildlife Service.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. Ecology letters, 8, 993-1009.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. Ecological modelling, 135, 147-186.

Habersack, H. M. (2000). The river-scaling concept (RSC): a basis for ecological assessments. Hydrobiologia, 422, 49-60.

Hawaii Stream Assessment (1991). A preliminary appraisal of Hawaii's stream resources. Prepared for the Commission on Water Resources Management. Hawaii Cooperative Park Service Studies Unit. Honolulu, HI.

Hawkins, C.P., Kershner, J.L., Bisson, P.A., Bryant, M.D., Decker, L.M., Gregory, S.V., McCullough, D.A., Overton, C.K., Reeves, G.H., Steedman, R.J. & Young, M.K. (1993). A hierarchical approach to classifying stream habitat features. Fisheries, 18, 3-12.

Herborg, L. M., Mandrak, N. E., Cudmore, B. C., & MacIsaac, H. J. (2007). Comparative distribution and invasion risk of snakehead (Channidae) and Asian carp (Cyprinidae) species in North America. Canadian Journal of Fisheries and Aquatic Sciences, 64(12), 1723-1735.

Hernández, M.R., & Bückle, L.R. (2002). Temperature tolerance polygon of Poecilia sphenops Valenciennes (Pisces: poeciliidae). Journal of Thermal Biology, 27, 1-5.

Higashi, G. R., & Nishimoto, R. T. (2007). The point quadrat method: a rapid assessment of Hawaiian streams. Bishop Museum Bulletins in Cultural and Environmental Studies, 3, 305-313.

Hollander, M., & Wolfe, D. A. (1973). Nonparametric Statistical Methods. New York: John Wiley & Sons, 185–194.

Holitzki, T. M., MacKenzie, R. A., Wiegner, T. N., & McDermid, K. J. (2013). Differences in ecological structure, function, and native species abundance between native and invaded Hawaiian streams. Ecological Applications, 23, 1367-1383.

Huner, J. V., & Barr, J. E. (1991). Red Swamp Crawfish: Biology and Exploitation; Louisiana Sea Grant College Program. Center for Wetland Resources, Lousiana State University.

Jackman, S., (2017). pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory. United States Studies Centre, University of Sydney. Sydney, New South Wales, Australia. R package version 1.5.1. URL https://github.com/atahk/pscl/

Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., & Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. Biological invasions, 13, 2785-2797.

Jongman, R. H. G., Ter Braak, C. J., & Van Tongeren, O. F. (1995). Data analysis in community and landscape ecology. Cambridge university press.

Keith, P. (2003). Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the Caribbean regions. Journal of Fish Biology, 63, 831-847.

Layhee, M., Marchetti, M. P., Chandra, S., Engstrom, T., & Pickard, D. (2014). Impacts of aquatic invasive species and land use on stream food webs in Kaua'i, Hawai'i. Pacific Conservation Biology, 20, 252-271.

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., & Brosse, S. (2008). Fish invasions in the world's river systems: when natural processes are blurred by human activities. PLoS Biology, 6, 28.

Lepš, J., & Hadincová, V. (1992). How reliable are our vegetation analyses?. Journal of Vegetation Science, 3, 119-124.

Lepš, J., & Šmilauer, P. (2003). Multivariate analysis of ecological data using CANOCO. Cambridge university press.

Lillywhite, H. B. (1970). Behavioral temperature regulation in the bullfrog, *Rana catesbeiana*. Copeia, 158-168

Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. Ecography, 28, 385-393.

Loope, L. L., Howarth, F. G., Kraus, F., & Pratt, T. K. (2001). Newly emergent and future threats of alien species to Pacific birds and ecosystems. Studies in Avian Biology, 22, 291-305.

Lyons, J., Stewart, J. S., & Mitro, M. (2010). Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, USA. Journal of Fish Biology, 77, 1867-1898.

Maciolek, J. A. (1984). Exotic fishes in Hawaii and other islands of Oceania (W. C. Junior, Ed.). In Distribution, biology, and management of exotic fishes (131-161). Baltimore: Johns Hopkins University Press.

Magurran, A. E. (2005). Evolutionary ecology: the Trinidadian guppy. Oxford University Press on Demand.

Maloney, K. O., Weller, D. E., Michaelson, D. E., & Ciccotto, P. J. (2013). Species distribution models of freshwater stream fishes in Maryland and their implications for management. Environmental Modeling & Assessment, 18, 1-12.

Marsh-Matthews, E., & Matthews, W. J. (2000). Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States?. Ecology of Freshwater Fish, 9, 9-21.

Martin, S. B., Hitch, A. T., Purcell, K. M., Klerks, P. L., & Leberg, P. L. (2009). Life history variation along a salinity gradient in coastal marshes. Aquatic Biology, 8, 15-28.

Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., Tyre, A.J, & Possingham, H. P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters, 8, 1235-1246.

McDowall, R. M. (1995). Seasonal pulses in migrations of New Zealand diadromous fish and the potential impacts of river mouth closure. New Zealand journal of marine and freshwater research, 29, 517-526.

McDowall, R. M. (2003). Hawaiian biogeography and the islands' freshwater fish fauna. Journal of Biogeography, 30, 703-710.

McDowall, R. M. (2007). Hawaiian stream fishes: the role of amphidromy in history, ecology and conservation biology. Bishop Museum Bulletin in Cultural and Environmental Studies, 3, 3-9.

McKinney, M. L. (2002). Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. Diversity and Distributions, 8, 311-318.

McNyset, K. M. (2005). Use of ecological niche modelling to predict distributions of freshwater fish species in Kansas. Ecology of Freshwater Fish, 14, 243-255.

McRae, M. G., McRae, L. B., & Fitzsimons, J. M. (2013). Microhabitat use in an Assemblage of Native and Introduced Fishes in a Hawaiian Stream 1. Pacific Science, 67, 205-217.

Montgomery, D. R. (1999). Process domains and the river continuum. American Water Resources Association, 35, 397-410.

Murthy, V. K., Reddanna, P., & Govindappa, S. (1981). Hepatic carbohydrate metabolism in *Tilapia mossambica* (Peters) acclimated to low environmental pH. Canadian Journal of Zoology, 59, 400-404.

National Oceanic and Atmospheric Administration, Office for Coastal Management. "State of Hawaii 2010-2011" Coastal Change Analysis Program (C-CAP) High-Resolution Land Cover. Charleston, SC: NOAA Office for Coastal Management. Accessed at www.coast.noaa.gov/ccapftp.

Nico, L. G., & Walsh, S. J. (2011). Non-indigenous freshwater fishes on tropical Pacific islands: a review of eradication efforts. In Island Invasives: eradication and management. Proceedings of the International Conference on Island Invasives. International Union for Conservation of Nature, Gland, Switzerland (Vol. 97107).

Norton, S. E., Timbol, A. S., & Parrish, J. D. (1978). Stream channel modification in Hawaii. Part B: Effect of channelization on the distribution and abundance of fauna in selected streams (No. FWS/OBS-78/77 Final Report).

Oakes, R. M., Gido, K. B., Falke, J. A., Olden, J. D., & Brock, B. L. (2005). Modelling of stream fishes in the Great Plains, USA. Ecology of Freshwater Fish, 14, 361-374.

Oki, D.S. (2004). Trends in streamflow characteristics at long-term gaging stations, Hawaii (No. 2004-5080). United States Geological Survey.

Oki, D. S., & Brasher, A. M. (2003). Environmental setting and the effects of natural and human-related factors on water quality and aquatic biota, Oahu, Hawaii (No. 2003-4156). United States Geological Survey.

Oki, D. S., Rosa, S. N., & Yeung, C. W. (2010). Flood-Frequency Estimates for Streams on Kaua ‘i, O ‘ahu, Moloka ‘i, Maui, and Hawai ‘i, State of Hawai ‘I (No. 2010–5035). United States Geological Survey.

Peterson, A. T. (2003). Predicting the geography of species’ invasions via ecological niche modeling. The quarterly review of biology, 78, 419-433.

Pahl-Wostl, C. (1998). Ecosystem organization across a continuum of scales: a comparative analysis of lakes and rivers. Ecological Scale: Theory and Applications, 141-179.

Philippart, J. C., & Ruwet, J. C. (1982). Ecology and distribution of tilapias. The Biology and Culture of Tilapias, 7, 15-60.

Poff, N. L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. North American Benthological Society, 16, 391-409.

Potts, J. M., & Elith, J. (2006). Comparing species abundance models. Ecological Modelling, 199, 153-163.

Qian, S. S., King, R. S., & Richardson, C. J. (2003). Two statistical methods for the detection of environmental thresholds. Ecological Modelling, 166, 87-97.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical computing. Vienna, Austria. Version 3.4.0.

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of biogeography, 41, 629-643.

Rappaport, U., Sarig, S., & Marek, M. (1976). Results of tests of various aeration systems on the oxygen regime in the Genosar experimental ponds and growth of fish there in 1975. Bamidgeh, 28, 35-49.

Sanderson, M. (1993). Prevailing trade winds: climate and weather in Hawaii. University of Hawaii Press.

Schlosser, I. J. (1991). Stream fish ecology: a landscape perspective. BioScience, 41, 704-712.

Seidl, M. A., Dietrich, W. E., & Kirchner, J. W. (1994). Longitudinal profile development into bedrock: An analysis of Hawaiian channels. Geology, 102, 457-474.

Senguttuvan, M., & Sivakumar, A. A. (2002). Effect of air-exposure on the blood parameters of *Oreochromis mossambicus* (Peters). Himalayan Journal of Environment and Zoology, 16, 15-21.

Shafland, P. L. (1991). Management of introduced freshwater fishes in Florida. In New directions in research, management and conservation of Hawaiian freshwater stream ecosystems: proceedings of the 1990 symposium on freshwater stream biology and fisheries management. Division of Aquatic Resources, Department of Land and Natural Resources, Honolulu (213-237).

Sharma, S., Herborg, L. M., & Therriault, T. W. (2009). Predicting introduction, establishment and potential impacts of smallmouth bass. Diversity and Distributions, 15, 831-840.

Smith, A. M., & Green, D. M. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations?. Ecography, 28, 110-128.

Smith, G. C., Covich, A. P., & Brasher, A. M. (2003). An ecological perspective on the biodiversity of tropical island streams. AIBS Bulletin, 53, 1048-1051.

Snow, N., & Witmer, G. (2010). American bullfrogs as invasive species: a review of the introduction, subsequent problems, management options, and future directions. USDA National Wildlife Research Center - Staff Publications.

Staples, G., & Cowie, R. H. (2001). Hawai‘i's invasive species. Mutual Publishing, Honolulu, Hawaii.

Stauffer, J. R. (1986). Effects of salinity on preferred and lethal temperatures of the *Mozambique tilapia*, *Oreochromis mossambicus* (Peters). American Water Resources Association, 22, 205-208.

Steen, P. J., Zorn, T. G., Seelbach, P. W., & Schaeffer, J. S. (2008). Classification tree models for predicting distributions of Michigan stream fish from landscape variables. Transactions of the American Fisheries Society, 137, 976-996.

Symonds, M. R., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology, 65, 13-21.

Ter Braak, C. J. F., & Smilauer, P. (2012). CANOCO reference manual and user's guide: software for ordination (version 5.0). Biometris.

Tingley, R. W. III (2017). Conserving streams with changing climate: a multi-scaled research framework to consider current and future conditions of Hawaiian stream habitats. Doctoral dissertation, University of Michigan.

Timbol, A. S., & Maciolek, J. A. (1978). Stream channel modification in Hawaii. Part A: Statewide inventory of streams, habitat factors and associated biota (No. FWS/OBS-78/16 Final Rpt.).

Torres Dowdall, J., Handelsman, C. A., Ruell, E. W., Auer, S. K., Reznick, D. N., & Ghalambor, C. K. (2012). Fine-scale local adaptation in life histories along a continuous environmental gradient in Trinidadian guppies. Functional Ecology, 26, 616-627.

Townsend, C. R., Doledec, S., Norris, R., Peacock, K., & Arbuckle, C. (2003). The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. Freshwater Biology, 48, 768-785.

Townsend, C. R., & Hildrew, A. G. (1994). Species traits in relation to a habitat templet for river systems. Freshwater biology, 31, 265-275.

Tsang, Y. P., Wieferich, D., Fung, K., Infante, D. M., & Cooper, A. R. (2014). An approach for aggregating upstream catchment information to support research and management of fluvial systems across large landscapes. SpringerPlus, 3, 589.

U.S. Department of Agriculture (2013). National SSURGO data: Natural Resources Conservation Service, accessed at http://www.ncgc.nrcs.usda.gov/branch/ssb/products/ssurgo/data/hi.html.

Walter, R. P., Hogan, J. D., Blum, M. J., Gagne, R. B., Hain, E. F., Gilliam, J. F., & McIntyre, P. B. (2012). Climate change and conservation of endemic amphidromous fishes in Hawaiian streams. Endangered Species Research, 16, 261-272.

Ward, J. V., & Palmer, M. A. (1994). Distribution patterns of interstitial freshwater meiofauna over a range of spatial scales, with emphasis on alluvial river-aquifer systems. Hydrobiologia, 287, 147-156.

Ward, J. V., Tockner, K., Arscott, D. B., & Claret, C. (2002). Riverine landscape diversity. Freshwater Biology, 47, 517-539.

Warren, D. L., & Seifert, S. N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological applications, 21, 335-342.

Wang, L., Lyons, J., Kanehl, P., & Bannerman, R. (2001). Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management, 28, 255-266.

Wang, L., Lyons, J., Rasmussen, P., Kanehl, P., Seelbach, P., Simon, T., Wiley, M., Baker, E., Niemela, S. and Stewart, M. (2003). Influences of landscape-and reach-scale habitat on stream fish communities in the Northern Lakes and Forest ecoregion. Canadian Journal of Fisheries and Aquatic Science, 60, 491-505.

Wang, L., Infante, D., Esselman, P., Cooper, A., Wu, D., Taylor, W., Beard, D., Whelan, G. and Ostroff, A. (2011). A hierarchical spatial framework and database for the national river fish habitat condition assessment. Fisheries, 36, 436-449.

Wiens, J. A. (2002). Riverine landscapes: taking landscape ecology into the water. Freshwater biology, 47, 501-515.

Yamamoto, M. N., & Tagawa, A. W. (2000). Hawai'i's Native & Exotic Freshwater Animals. Mutual Publishing, Honolulu, Hawaii.

Zeileis, A., Kleiber, C., & Jackman, S. (2008). Regression models for count data in R. Journal of statistical software, 27, 1-25.

Zhang, C., Wang, Y., Hamilton, K., & Lauer, A. (2016). Dynamical downscaling of the climate for the Hawaiian Islands. Part II: Projection for the late twenty-first century. Journal of Climate, 29, 8333-8354.