OREGON SPOTTED FROG (*Rana pretiosa)* ABSENCE IN THE CHEHALIS RIVER BASIN:

AN ANALYSIS OF HABITAT, CLIMATE AND INVASIVE SPECIES

by

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ABSTRACT

Oregon Spotted Frog (*Rana pretiosa)* Absence in the Chehalis River Basin: An Analysis of Habitat, Climate, and Invasive Species

Patrick Murtagh

The Oregon spotted frog (*Rana pretiosa*) is a federally threatened and Washington state endangered species now extirpated from close to 80% of its historical range (from British Columbia to Northern California). This loss is attributed to habitat loss, invasive species, disease and climate change. In Washington state, there are six drainages currently known to have populations of frogs and only one in the South Puget Sound: the Black River. The Black River is a tributary of the Chehalis River, which despite being aquatically linked to the Black River, has no records of Oregon spotted frog occurrence. One of the recovery objectives for the Oregon spotted frog is to locate new populations, potentially in the Chehalis River Basin. Prior to this study, amphibian surveys had been conducted in the Chehalis River mainstem floodplain, all of which failed to detect Oregon spotted frog.

To determine the extent of suitable habitat in the Chehalis River Basin, habitat was modelled using the Maxent species distribution model and the environmental variables and presence of invasive species (centrarchid fishes and American Bullfrog) were compared between the watersheds. The Maxent model located suitable habitat throughout the Chehalis Basin by finding locations with similar habitat to the Black River watershed. Surveyed locations in the Chehalis River floodplain, that were deemed as suitable habitat, were compared to occupied locations in the Black River by their habitat structure, climate and abundance of invasive species. According to this comparison, the habitat structure of the Chehalis River is not a limiting factor for Oregon spotted frog. The climate and abundance of invasive species were different between the rivers, yet there is stronger evidence to suggest that the presence of American Bullfrogs and centrarchid fishes (invasives) are having a greater effect towards the presumed absence of Oregon spotted frog in the Chehalis River Basin outside of the Black River.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

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INTRODUCTION

The Oregon spotted frog (*Rana pretiosa*) is a ranid frog endemic to the Pacific Northwest. Historically, they occupied territory from British Columbia, to Northern California, however, this range has been reduced by up to 80% (Adams et al., 2014; Hayes, 1997). This large reduction in range has led to a threatened listing under the Endangered Species Act and an endangered listing in Washington state. They are wetland specialists with a complex life cycle; occupying multiple aquatic habitats including seasonally flooded shallows for oviposition, permanent water during the dry season, and springs, beaver dams or flowing water for over-wintering (Pearl & Hayes, 2004). These habitats and the frog are at risk from altered hydrology, invasive species, disease and climate change (Hallock, 2013; Holgerson et al., 2019; Watson et al., 2003).

Of particular concern, are the challenges imposed on the Oregon spotted frog by the introduction of invasive species and the alteration of the natural hydrology of many of Washington's wetlands. When waterways are channelized to reduce flooding or convert wetlands to agriculture, they become static and the seasonal hydrological fluctuations necessary for the Oregon spotted frog are removed (McAllister & Leonard, 1997). The invasive species of concern for the Oregon spotted frog include aquatic fauna, specifically the American bullfrog (*Lithobates catesbeianus*) and centrarchid fishes (Holgerson et al., 2019). Centrarchids are warmwater fish of the sunfish family introduced into many of Washington's rivers for sport fishing (Hallock, 2013). Invasive species increase predation pressure, are able to outcompete for resources and create barriers to migration, thus isolating populations (Bradford & Tabatabai, 1993; Pearl & Hayes, 2004). Many native amphibians in the Pacific Northwest are vulnerable to these species but especially the Oregon spotted frog. Due to their aquatic nature and inability to escape into terrestrial habitat like other native amphibians, frogs are forced to share a larger proportion of their habitat and thus increase their interactions with these invasive species (Holgerson et al., 2019; Rowe et al., 2021).

In Washington state, there are six drainages that are currently known to have populations of Oregon spotted frog, of which, the Black River is the only watershed in the South Puget Sound (Hallock, 2013). The Black River is a tributary of the Chehalis River, and due the aquatic connectivity and size of the larger Chehalis Basin, frogs may have occurred in other reaches of this watershed. However, there has never been a recorded occurrence of Oregon spotted frog elsewhere in the Chehalis Basin (M. Hayes, personal communication). The Black River may be unique among the Chehalis tributaries as it has one of the largest intact freshwater wetland systems remaining in the Puget Sound region, making it ideal habitat for the Oregon spotted frog (Species Restoration Plan Steering Committee, 2019).

Successful conservation efforts of rare or sensitive species depend on knowledge of the habitat requirements and the current distribution of the species of interest (Bohannon et al., 2016). As such, one of the Oregon spotted frog recovery objectives proposed by the Washington Department of Fish and Wildlife is to locate new populations for this reason (Hallock, 2013). Despite the lack of occurrences, there is potential for discovery of previously undocumented population in Chehalis Basin due to the connection to the Black River and the wide array of habitat found in such a large watershed.

In this study, suitable Oregon spotted frog breeding habitat was modeled in the Chehalis Basin using the species distribution model, Maxent. The Maxent model used the habitat conditions of locations in the Black River with known Oregon spotted frog presence and modelled areas of similar conditions elsewhere in the Chehalis Basin. Suitable habitat was predicted in the Chehalis River floodplain itself, as well as among many of its tributaries. Further, using the habitat model as a guide, prior surveyed locations in the Chehalis River floodplain that were deemed as suitable habitat were compared to known breeding locations in the Black River. These locations were compared by their habitat structure, climate, and abundance of invasive bullfrogs and centrarchids. The purpose of this comparison was to detect any difference between the two rivers to better explain the presumed absence of Oregon spotted frog outside of the Black River.

LITERATURE REVIEW

The Oregon Spotted Frog

The Oregon spotted frog (*Rana pretiosa*) is a ranid frog endemic to the Pacific Northwest. Historically, they occupied territory from British Columbia to Northern California, however, they are now believed to be missing from close to 80% of this range (Adams et al., 2014; Groff et al., 2014; Hayes, 1997). Because of this large range reduction, the Oregon spotted frog is listed as threatened under the US Endangered Species Act. At the state level, Oregon spotted frog is designated as endangered in Washington and Canada, sensitive in Oregon and believed extirpated from California. The loss of Oregon spotted frog from this territory can be attributed to habitat loss or conversion, the introduction of invasive species, and disease; all of which have the potential to be exacerbated by climate change (Hallock, 2013; Holgerson et al., 2019; McAllister & Leonard, 1997).

In Washington state, Oregon spotted frogs historically occupied at least fifteen different watersheds. Currently, they are known to exist in just four watersheds in the Puget Sound: the Samish River, Black Slough, Sumas River, and the Black River, and two in the Eastern Cascades: Trout Lake Creek and Outlet Creek (Figure 1). Conboy Lake National Wildlife Refuge, part of the Outlet Creek drainage, supports one of the largest populations in the entire range (Bohannon et al., 2016; Hallock, 2013; McAllister & Leonard, 1997). While the Black River is a tributary of the Chehalis River, there are no records of Oregon spotted frogs ever occurring anywhere else in the Chehalis River Basin (M. Hayes, Personal communication). Outside of Washington state, Oregon spotted frogs currently occupy sites in the Fraser Valley in British Columbia and in the Oregon Cascades (Hallock, 2013; McKibbin et al., 2008).

Figure 1. The watersheds in Washington state currently known to have populations of Oregon spotted frog.

Figure 1. The watersheds in Washington state currently known to have populations of Oregon spotted frog.

Life History

Non-Breeding Habitat

Oregon spotted frog are strictly aquatic, warmwater wetland specialists occupying a variety of habitat types depending on lifecycle stage or season (Pearl & Hayes, 2004). Their habitat varies depending on the breeding, non-breeding, and over-wintering season (Watson et al., 2003). To meet this diverse need, occupied wetlands tend to be at least four hectares in size and contain perennial streams and water bodies aquatically connected to areas of seasonal inundation (Pearl & Hayes, 2004; Watson et al., 2000). A gradual topographic gradient sloping towards the permanent waterway is ideal to allow for the persistent and required water levels used during the year (Watson et al., 2000). Wetland systems used by the Oregon spotted frog are palustrine and lacustrine (Bohannon et al., 2016). Palustrine systems are shallow, permanent or temporary, vegetated wetlands found on the edges and floodplains of rivers, lakes or ponds. Marshes, swamps, bogs, prairies and fens are all palustrine systems. The emergent vegetation, plants that root in the soil of aquatic environments but grow above the water level, in these systems is different than that of the vegetation in running or permanent, deeper water (Cowardin et al., 1979). Lacustrine systems are deeper than palustrine and tend to be more permanent. They are formed by dammed rivers and depressions (Cowardin et al., 1979). Palustrine, emergent wetlands are the primary system occupied by Oregon spotted frog. Wetland complexes that have multiple habitat types are more likely to be occupied. (Pearl & Hayes, 2004).

During the non-breeding season, Oregon spotted frogs reside in permanent, usually deeper water, unlike the seasonally inundated shallow areas used during the breeding season (Watson et al., 2000, 2003). During the summer months, water temperatures in these permanent waterways typically exceeds 20 °C (Hayes, 1994). These deeper pools contain sparse to moderate emergent vegetation, often hardhack (*Spirea douglasii*) dominated, and vegetative mats; on which they can float and bask (McAllister & Leonard, 1997; Watson et al., 2003) The vegetation allows for cover and escape from predators, while the mats offer better thermal regulation as they can move from the warmer, shallower water created by the mats or to deeper water depending on temperature needs. (McAllister & Leonard, 1997; Popesu et al., 2013; Watson et al., 2000). Oregon spotted frogs will either swim in the deep water or crawl across the mats to ambush prey, mainly consisting of aquatic breeding insects (Pearl et al., 2005).

There is flexibility in Oregon spotted frog habitat selection during this season, both in water depth, such as deep pools or shallow flooded fields, and among what dominant vegetation, usually sedge or shrub-scrub, but the availability of water remains the limiting factor (Watson et al., 2000). As seasonal water levels recede, frogs will stay in permanent pools, only venturing out if wetter conditions provide temporary flooding of surrounding areas and corridors between habitat types (McAllister & Leonard, 1997; Popesu et al., 2013; Watson et al., 2003). This need for both aquatic habitat and corridors can constrain frogs to small areas during the summer if drier conditions prevent adequate water levels for movement (Popesu et al., 2013; Watson et al., 2003).

Oregon spotted frogs use water temperature as a sign of changing seasons and will move to overwintering habitat along aquatic corridors as the temperature begins to lower. In the colder regions of their range, water temperatures approaching five degree Celsius cue the frogs to find suitable habitat before the more extreme winter conditions occur. (Hayes et al., 2001; Pearl et al., 2018). Overwintering habitat for the Oregon spotted frog requires adequate levels of dissolved oxygen and cover from predators (Hayes et al., 2001). Dissolved oxygen levels will be lower in water that is iced-over, therefore overwintering in springs and beaver dams can allow flowing water to prevent hypoxic conditions and lessen the chance of freezing. However, if under ice, frogs will move around to find pockets of higher oxygenated water (Hallock, 2013; Hayes et al., 2001; Pearl et al., 2018). The absence of predators in overwintering sites is important and can include fish, birds, minks and otters (Chelgren et al., 2008; Hayes et al., 2001; Pearl et al., 2018; Watson et al., 2000). Cover from predators can be found in beaver dams and bank hollows (Pearl et al., 2018; Tattersall & Ultsch, 2008).

These different habitat types need to exist within a relatively small distance as frogs do not disperse over large areas. They need to be connected by aquatic corridors, thus wetland complexes that contain multiple habitat types are ideal (Pearl & Hayes, 2004). Habitat elements that exist in isolation will not be available to the frogs, such as a disconnected pool or shallow flooded areas that are not connected to a perennial water source (Watson et al., 2000). Frogs may migrate between populations or colonize new areas that are aquatically connected to their home ranges (Watson et al., 2003).

Breeding Habitat

In late winter and early spring, as water temperatures begin to consistently rise above 5 °C, Oregon spotted frogs will move out to breeding sites to begin oviposition (Bowerman & Pearl, 2020; Licht, 1974; Mcallister & White, 2001; Pearl & Hayes, 2004). Reliance on environmental cues, as opposed to calendar dates, give the frogs flexibility for starting migration and breeding and can therefore avoid large mortality events. These events can occur when moving away from overwintering sites too early and freezing, too late and leaving eggs stranded in drier conditions, or exposing themselves to predators while at the breeding site (Bowerman & Pearl, 2020). Transitioning from overwintering sites, frogs move out into shallow, lentic water to begin oviposition (McAllister & Leonard, 1997; Pearl & Hayes, 2004; Tattersall & Ultsch, 2008;

Watson et al., 2003). Oregon spotted frog are communal breeders and have a high site fidelity, often returning to the same site each year to lay egg masses in groups of varying sizes (Licht, 1971; Pearl & Hayes, 2004).

Because of Oregon spotted frog's aquatic nature, areas of temporary shallow water, such as floodplains and seasonal wetlands, must have a hydrological connection to a permanent waterway (Watson et al., 2003). Shallow water depth, typically less than 25 cm, is critical for oviposition, therefore, these sites are often located near the margins of seasonally inundated floodplains or near the shores of ponds, but small depressions or even tire tracks may be sufficient (Licht, 1971; McAllister & Leonard, 1997; Mcallister & White, 2001; Pearl, Adams, et al., 2009; Pearl & Hayes, 2004; Watson et al., 2000, 2003). Temperatures are warmer in shallow water, which aids in incubating egg masses (Mcallister & White, 2001; Pearl, Adams, et al., 2009). However, these temporary shallows create potential for large mortality events if water recedes too quickly and egg masses are left to desiccate or tadpoles and juvenile frogs are unable to reach permanent water in the drier season due to lack of aquatic connections (Licht, 1974; Pearl & Hayes, 2004; Watson et al., 2003).

Breeding sites are mostly located in palustrine wetlands among emergent vegetation or aquatic beds (Bohannon et al., 2016; Pearl & Hayes, 2004). These areas typically have moderate to low density vegetation with open canopies to prevent shading and allow for more surface exposure to the sun (Kapust et al., 2012; Watson et al., 2003). The dominant vegetation at oviposition sites is often a mix a sedges and rushes, however, the structure of the vegetation is more important than the species and frogs will lay egg masses atop denser vegetated substrates if the density and height of the surrounding vegetation is low enough to provide adequate sun exposure (McAllister & Leonard, 1997; Pearl & Hayes, 2004; Watson et al., 2000, 2003).

Suitable vegetation structures mimic early successional stages with short heights and low densities, however, with a lack of natural openings or disturbance, conditions can be found from light grazing, winter snowpack flattening and compressing the vegetation, or human activities such as mowing or haying (Hallock, 2013; Kapust et al., 2012; Watson et al., 2003).

Beaver dams have the potential to create and expand Oregon spotted frog habitat. The resulting hydrology from beaver dams satisfy many of the requirements for the Oregon spotted frog lifecycle. The increase of permanent water behind the dam, the resulting flooding of adjoining fields and meadows, and the shelter provided during overwintering are all critical elements of the lifecycle (Hallock, 2013; Pearl et al., 2018; Romansic et al., 2020).

Threats to the Oregon Spotted Frog

Amphibians are in decline worldwide (Stuart et al., 2004). In the United States, surveys of species that have a threat designation, such as threatened or endangered, show a continual decline across their ranges (Adams et al., 2013). Sources of the decline comes from habitat loss, invasive species, climate change, and disease, specifically the fungal disease *Batrachochytrium dendrobatidis* (Bd) (Wake & Vredenburg, 2008). Human interference can be attributed to many of the threats posed to amphibians, including altering the hydrology and destroying habitat, introducing invasive species and contributing to climate change (Arkle & Pilliod, 2015; Wake & Vredenburg, 2008). In the Pacific Northwest, aquatic amphibians, including Oregon spotted frog, face challenges from disease, habitat loss, altered hydrology from the removal of beaver (*Castor canadensis*) and human interference, climate change and the introduction of invasive plant and animal species (Arkle & Pilliod, 2015; Hallock, 2013; Hayes et al., 2009; Pearl, Adams, et al., 2009). The species that are most adversely affected by these threats occur in small population sizes in habitat that is located in areas undergoing human encroachment and development (Wake & Vredenburg, 2008).

The Oregon spotted frog lifecycle naturally lends itself to high mortality events and population fluctuations due to communal breeding activities. High reproductive mortality can occur when disturbances affect egg masses concentrated in a small area or when frogs congregate at the breeding site and are exposed to high predation events (Chelgren et al., 2008; Mcallister & White, 2001). These natural fluctuations combined with isolated populations and novel interferences are contributing to the decline of the Oregon spotted frog (Blouin et al., 2010; Pearl & Hayes, 2004).

Habitat Conversion and Hydrology Changes

One of the major causes of Oregon spotted frog decline is the loss of suitable habitat from altered hydrology and disturbance regimes. The lowland floodplains and wetlands inhabited by Oregon spotted frog are readily converted to agricultural and livestock fields (McAllister & Leonard, 1997). These conversions are accomplished by channelizing, draining and dredging wetlands and marshes, and the resulting hydrology can no longer support Oregon spotted frog (Hallock, 2013; McAllister & Leonard, 1997). The channelized waterways prevent seasonal flooding and diminish areas of sustained water, thus eliminating aquatic corridors between different populations and local habitat types (Cushman, Kathleen & Pearl, Christopher, 2007; Watson et al., 2000, 2003). Isolated populations with no means of reaching other populations will experience genetic diversity loss (Blouin et al., 2010; Cushman, Kathleen & Pearl, Christopher, 2007; McKibbin et al., 2008). Human control of water flows can lead to drastic changes in the water levels of Oregon spotted frog habitat and can strand egg masses or tadpoles if levels recede too rapidly (Hallock, 2013; McAllister & Leonard, 1997).

The increase of human presence in Oregon spotted frog habitat has led to a decline in disturbance responsible for resetting wetlands to early successional stages. Fire has been removed from many natural systems following European settlement and flood events have decreased due to the channelization of many waterways and removal of beavers (Hallock, 2013). The absence of these disturbances has accelerated the establishment of woody plants and succession into upland habitat not favored by Oregon spotted frogs (Cushman, Kathleen & Pearl, Christopher, 2007; Hayes, 1997). Additionally, human restoration actions in many wetlands involve planting woody species to benefit salmon, thus further reducing habitat for frogs (Bohannon et al., 2016; Hallock, 2013). The increased cover from woody plants increases the vegetation height and thus decreases the solar exposure relied upon for egg mass incubation and warmer water temperatures.

Many sites now occupied by Oregon spotted frog are maintained by human activities such as mowing or livestock grazing (Hallock, 2013; Kapust et al., 2012). Intensive grazing can be detrimental to wetlands but moderate to light grazing mimics natural disturbance at many Oregon spotted frog occupied sites by keeping vegetation heights and densities low and preventing the establishment of woody species (Bohannon et al., 2016; Hayes, 1997; McAllister & Leonard, 1997; Watson et al., 2000, 2003). Oregon spotted frogs breed more often in grazed areas when the natural vegetation structure has been altered from lack of disturbance or the introduction of invasive species such as reed canary grass (*Phalaris arundinacea*) (Bohannon et al., 2016; Watson et al., 2003). The cessation of grazing at many Oregon spotted frog sites has led to a decline in populations due to the reestablishment of invasive vegetation (Bohannon et al., 2016; Hallock, 2013).

Invasive Species

Reed canary grass is a prolific invader of wetlands in the Pacific Northwest and aggressively colonizes and degrades Oregon spotted frog habitat. It establishes rapidly after disturbance and grows under a variety of environmental conditions and growth patterns (Reinhardt Adams & Galatowitsch, 2005). This flexibility allows it to outcompete many native species, including the sedges and rushes used by the Oregon spotted frog (Lavergne & Molofsky, 2004; Watson et al., 2003). Reed canary grass does not establish well under a shaded canopy but is more successful in wetlands at an early stage of succession with no canopy and low vegetation density (Maurer et al., 2003). Disturbance and the resulting early successional stage wetlands such as these are ideal habitat for Oregon spotted frog and thus reed canary grass is a major contributor to the decline in available habitat (Hallock, 2013). As abundance of reed canary grass increases, the structure of the vegetation community changes with increasing density, height, and thatch and litter depth (Spyreas et al., 2010). These altered vegetation characteristics run counter to the breeding site preferences of Oregon spotted frog and they will no longer use these sites if reed canary grass is prevalent at high densities (Bohannon et al., 2016; Watson et al., 2003). If sites occupied by Oregon spotted frog are invaded by reed canary grass, frogs are forced to seek out new areas that are less dense and will not hamper movement (Popesu et al., 2013). Because the structure of the vegetation is more important than the specific species, oviposition may still occur among reed canary grass if there are large enough openings. These openings may be caused by snow compaction, grazing or other human interventions that mimic the short, sparse vegetation characteristics preferred by the frog (Hallock, 2013; Kapust et al., 2012; Watson et al., 2003).

Oregon spotted frog is an important food source for many native species, however, the increased predation threat and habitat overlap from nonnative species amplifies pressure on small populations and can act as a barrier to movement between aquatic habitats (Bradford & Tabatabai, 1993). The occurrence of exotic fish and bullfrogs has been associated with reduced presence or absence of native amphibians in the Pacific Northwest (Holgerson et al., 2019; Pearl et al., 2004). Oregon spotted frog is particularly at risk of these species due to its completely aquatic lifecycle. Frogs cannot escape predators by retreating to terrestrial habitat during the non-breeding season as many other native amphibians can (Holgerson et al., 2019).

The introduced American bullfrog (*Lithobates catesbeianus*) is problematic for many native Pacific Northwest frogs due to their opportunistic feeding behavior and large sized juvenile's ability to outcompete other species (Kiesecker & Blaustein, 1998; Pearl & Hayes, 2004). The American bullfrog shares similar habitat with the Oregon spotted frog and the resulting interaction can force Oregon spotted frog into suboptimal habitat (Pearl & Hayes, 2004; Rowe et al., 2021). This can result in reduced development in young frogs due to diminished water conditions or food sources for tadpoles. They can also be forced to retreat into areas where they interact with novel predators not normally encountered (Kiesecker & Blaustein, 1998).

Non-native fish can outcompete and feed on Oregon spotted frogs, especially during low water years and while in overwintering habitat. Further, they can cause Oregon spotted frogs to be forced out of preferred habitat by other non-native predators (Holgerson et al., 2019; Pearl, Adams, et al., 2009). An abundance of warmwater centrarchid fishes (i.e., basses and other sunfish) negatively affect native amphibian occurrence, especially in permanent water bodies (Hayes, 1997; Holgerson et al., 2019). These are fish that have been introduced into many of Washington's rivers for sport fishing (Hallock, 2013). When frogs move into different, potentially deeper, aquatic habitat they can encounter fish species that they would not normally interact with (Hallock, 2013; McAllister & Leonard, 1997; Pearl, Adams, et al., 2009).

Additionally, predatory fish can be agents of isolation because they do not allow frogs to move along aquatic corridors to reach new populations (Bradford & Tabatabai, 1993). The increase in human presence can introduce synanthropic predators such as raccoons and crows (Hallock, 2013).

Disease - Batrachochytrium dendrobatidis in the PNW

A lesser threat to Oregon spotted frog persistence is the fungal disease, *Batrachochytrium dendrobatidis* (Bd), which is attributed to global declines of amphibians (Wake & Vredenburg, 2008). Bd is prevalent throughout the Pacific Northwest and Oregon spotted frog has a high rate of infection in comparison with other amphibians in the region (Hayes et al., 2009; Pearl, Bowerman, et al., 2009). However, while infected frogs tend to be smaller, there is not a high rate of mortality (Padgett-Flohr & Hayes, 2011; Pearl, Bowerman, et al., 2009). This may be an artifact of the fungus being present for a long time in the region and frogs that survived today are the ones that are resistant to it (Padgett-Flohr & Hayes, 2011).

Climate Change

With a changing climate, wetlands in the Pacific Northwest are expected to experience increased temperatures and changing precipitation regimes (Hudec et al., 2019). These changes are expected to cause a shift in the hydrology of wetlands by changing the evapotranspiration rate, the duration of inundation, the seasonal water levels, and the groundwater recharge or depletion rate (Hallock, 2013; Hudec et al., 2019). However, many of these changes, and the effects they have on wetland species, is location dependent, affected by the local geology, climate, and surrounding land uses (Hudec et al., 2019). For example, a snow melt dependent system may experience more precipitation as rain, increasing stream inputs in the winter and fall instead of the spring and summer, or if neighboring agriculture is forced to draw more from groundwater storage during drier summers (Hallock, 2013; Hudec et al., 2019).

The Oregon spotted frog is considered highly vulnerable to climate change (Hohmann & Wall, 2017). While the effects of climate change are hard to predict, due to the aquatic nature of its entire life history, changes to the hydrology of wetlands will inevitably have effects on the frog. Increased temperatures and precipitation falling earlier and occurring as rain instead of snow pack, will shift historic water levels earlier in the year (Hallock, 2013). Coupled with more extreme winters, earlier springs can cause Oregon spotted frogs to mis-time their breeding, resulting in decreased reproductive success (Bowerman & Pearl, 2020). Shallow, ephemeral wetlands are at risk of not forming or drying quicker, thus stranding egg masses and tadpoles. Permanent wetlands can shrink in extent which will reduce available habitat for frogs during the drier months and allow for woody plants and reed canary grass to establish in the newly dried area (Hallock, 2013; Hudec et al., 2019). Oregon spotted frogs depend on aquatic corridors for migration, which will either shift in availability due to altered precipitation and drier summers, or not form at all and isolate populations and reduce gene flow (Robertson et al., 2018). A potential positive effect of climate change is the increased chance of disturbances, especially fire and flood events. These disturbances can reset wetlands to an early seral stage, ideal habitat for the Oregon spotted frog (Hudec et al., 2019).

Oregon Spotted Frog in the Chehalis River Basin

The Black River is one of the few remaining watersheds in Washington state to have Oregon spotted frogs. This tributary of the Chehalis River is connected aquatically to the greater

Chehalis River Basin, yet there are no historical records of frogs occurring outside of this watershed (M. Hayes, personal communication).

Oregon Spotted Frog Habitat

The Chehalis River Basin is the second largest river basin in Washington State behind the Columbia River, draining 2,600 square miles. Beginning in southern Lewis county, its runs north and west for 126 miles before ending in Grays Harbor (Thurston County Public Health and Social Services Department, 2006). It is primarily a rain driven system (Department of Ecology, 2016). Many of its major tributaries begin in forested headwaters and drain down to lower, more expansive floodplains. The tributaries nearer to the headwaters and middle of the Chehalis River contain palustrine wetland and prairie habitats, however the historic extent of these habitats has been reduced by development and agriculture. These tributaries include Salzer Creek, the Newakum River, the Skookumchuck River, Scatter Creek, the Black River, and the Satsop River (Department of Ecology, 2016; Species Restoration Plan Steering Committee, 2019). Wetlands in the Skookumchuck and Newakum Rivers have been reduced by 90 and 75 percent respectively. The Black River is an exception to this extensive habitat loss as it contains one of the largest intact wetland complexes in the Puget Sound (Species Restoration Plan Steering Committee, 2019).

Flowing out of Black Lake, near Tumwater, WA, The Black River meanders south for 28 miles, draining 136 square miles before joining the main stem of the Chehalis River (Dickes, 1990). The first seven miles south of Black Lake are protected riparian and wetland habitat. Combined with additional intact wetlands along the main stem and in multiple tributaries, the Black River watershed contains one of the largest contiguous, freshwater wetland complexes in the Puget Sound (Species Restoration Plan Steering Committee, 2019; Watson et al., 2000). The watershed was formed by retreating glaciers resulting in many areas of porous, glacial outwash soils. These porous soils and gentle gradients of many of the river's tributaries cause extensive groundwater flooding when the water table rises and they are unconfined in wetlands and agricultural fields (Thurston County Public Health and Social Services Department, 2006). This flooding and intact wetland habitat makes for ideal habitat for the Oregon spotted frog, making the Black River watershed one of the few rivers in Washington state and the only tributary in the Chehalis River Basin that the frog can be found (Species Restoration Plan Steering Committee, 2019).

Oregon Spotted Frog in the Black River

Oregon spotted frogs were first identified in the Black River during surveys of the Puget Sound in 1990 (McAllister et al., 1993). They have since been located in many other sites both along the Black River and in many of its tributaries. These include Allen Creek, Beaver Creek, Dempsey Creek, Fish Pond Creek, Michelle Creek, Mima Creek and Salmon Creek (Washington Deptartment of Fish and Wildlife, 2020).

Habitat Modelling

Species Distribution Models

Species distribution models (SDM) use the natural history and ecology of a species and combines them with statistical methods to explain the current and predicted species' distribution (Elith & Leathwick, 2009). They accomplish this by using locations with known species occurrences and combine them with relevant environmental variables to predict a distribution of similar environmental conditions across a targeted geographical area (Elith & Leathwick, 2009). SDMs are also known as ecological niche models as they model a species ecological niche within the studied environmental (Phillips et al., 2006). A species occupies a specific niche in the environment that contains elements for long term persistence without the need of immigration from other populations (Pulliam, 2000). The environmental niche is habitat suitable enough for a species to survive and reproduce in perpetuity. The fundamental niche is the entire collection of this suitable habitat and represents the geographic range available to this species, while the realized niche is the proportion of this available habitat that the species actually occupies (Pulliam, 2000). The difference between the fundamental niche and the realized niche can be attributed to external influences such as disturbance removing a population, competition from other species, and loss of connectivity between habitat (Phillips et al., 2006; Pulliam, 2000). A combination of environmental variables comprise the ecological niche, therefore, it is important to understand the ecology of the species of interest when choosing the environmental layers used in the model (Guisan & Thuiller, 2005). Different model approaches have been developed to incorporate either the realized nice or the fundamental niche when predicting suitable habitat; the difference being whether the model incorporates absences or just presences for the occurrence data.

Types of Species Distribution Models

Species distribution models can be classified as either presence-absence or presence-only depending on the type of occurrence data used in the model (Elith et al., 2011). Presence-absence models use inputs of both known presence locations and locations that were surveyed but no species were detected. Presence-only models use inputs of only known locations. There are advantages and disadvantages to using either model, but presence-only models perform better when species occurrence data is limited, especially in the case of threatened species where there are small numbers of populations (Cianfrani et al., 2010). Presence-absence models assume that the species is in equilibrium with the environment and all suitable habitat is occupied, thus using the fundamental nice as a model input. The assumption is that species are absent from sites because there is something key missing from that location (Guisan & Thuiller, 2005). Problems with this assumption occur when species are difficult to detect during surveys, corridors have been disrupted making suitable habitat unreachable to species with limited dispersal capacity, or a prior disturbance removed the population and they have been thus far unable to recolonize (Elith et al., 2006, 2011). SDMs are constrained to modelling in temporal space as well as geographic space, therefore, if a species has been removed in the past from suitable area, it should not be considered absent because in time they may recolonize. These factors can lead to false absences which result in false predictions of suitable habitat (Cianfrani et al., 2010).

Presence-only models remove the assumption of environmental equilibrium and only use the realized niche. Inputs are collected from the habitat that is currently being used, to predict the fundamental niche, the habitat that could be used (Phillips et al., 2006). These models have been shown to create better predictions for rare and threatened species as well as modelling potential recolonization areas. These potential recolonization area are missing from presence-absence models because they would have been inputted as absent from the start (Cianfrani et al., 2010; Elith et al., 2006).

However, there are some disadvantages to presence only modes. Presence-only models cannot predict the prevalence, the proportion of occurrences that occur at certain sites, of a species (Elith et al., 2011). Presence-only models are also more affected by sample bias, which occur when the sampling method favors areas either easily accessible to surveys due to geographic location, close to roads and towns, or access issues from private property (Boria et al., 2014; Elith et al., 2011). There is no way to know if areas that do not have occurrences are due to simply being unsampled, therefore the conditions at these sites may still be viable habitat. This bias can lead to spatial autocorrelation and overfitting of the model, leading predictions to favor the already known locations as these were the locations used when training the model (Boria et al., 2014). Models that are overfit will do poorly when new testing data is inputted into the model and will under-predict additional habitat beyond the original inputs (Radosavljevic & Anderson, 2014).

Maxent

Maxent is a presence-only model that performs well when compared to other SDMs (Ortega-Huerta & Peterson, 2008). Maxent is a species distribution model that estimates the probability of presence based on an index of habitat suitability across a targeted geographic area (Phillips et al., 2006). The model predicts presence at maximum entropy, or the maximum dispersal while being bounded by some environmental constraint (Phillips et al., 2006). The constraints are defined by the conditions of environmental variables, deemed ecologically relevant, at known locations of species presence. The details of how Maxent predicts habitat is described in the Methods section. The use of Maxent is widespread and a popular method of species distribution modelling.

Modelling for amphibians with Maxent

Maxent is a useful tool with a variety of uses in amphibian ecology. Compared to other modelling algorithms, Maxent is better at capturing the ecology of the species rather than solely being a result of statistical analysis (Preau et al., 2018). After all, species distribution models are meant to be an exercise in combining statistics with ecology, rather than a simple mathematical equation. Given the ability to perform well with small sample sizes, Maxent is useful for modelling distributions of amphibians with limited occurrence localities (Pearson et al., 2007;

Tarrant & Armstrong, 2013). The outputs of these models offer potential locations of conservation importance for endangered species and guide surveys for locating new populations of less studied species (Blank & Blaustein, 2012; Tarrant & Armstrong, 2013). Models created during different seasons or stages of the lifecycle can highlight migration patterns or species specific behaviors in amphibians (Najibzadeh et al., 2017). Additionally, Maxent works well with climate data. Like many species, amphibians have climatic restraints to their ranges and Maxent models can help define these (Cunningham et al., 2016). Amphibians tend to be less mobile than other taxa and are therefore face greater risks to climate or land use changes. Modelling with projected climate and land use conditions can define the loss or geographic shift in available habitat (Gül et al., 2018; Struecker & Milanovich, 2017).

Modelling for Oregon Spotted Frog

Prior modelling for Oregon spotted frog involved using a GIS "screen" to assess site suitability for the frog. These screens were created by combining data layers determined as ecologically relevant from literature studies. Layers include wetland type and size, soil type, elevation, and aquatic connectivity (Bohannon et al., 2016; Germaine & Cosentino, 2004). This method was applied in the North Puget Sound to successfully identify three new watersheds that contain previously undocumented populations, the Samish, Nooksack, and Sumas rivers (Bohannon et al., 2016). Maxent adds a statistical element to this type of ecological modelling (Na et al., 2018). It was used to predict potential populations in Southern Oregon and Northern California, where frogs are believed to be extirpated. Subsequent surveys of predicted locations did not find frogs in California, however, individual frogs were located in a previously undocumented location in Oregon which was predicted by the Maxent model (Groff et al., 2014).

When modelling for Oregon spotted frog with Maxent, the environmental variables need to reflect the frog's ecology, including limits on dispersal and habitat selection. Aquatic habitat is required at all life stages and is usually located among emergent wetlands (Pearl & Hayes, 2004). This habitat requirement can be represented in Maxent modelling by using land cover class and soil data. Hydric soils are formed under anaerobic conditions by permanent water or temporary flooding (Ecology, 1997). The distinction between hydric and non-hydric soils can delineate aquatic environments. The vegetation structure is another critical variable for breeding habitat selection, as frogs lay egg masses in areas of short statured vegetation that allows for exposure to air and solar radiation (Kapust et al., 2012; Watson et al., 2003). Habitat tends to be at lower elevations with higher water temperatures and gentle slopes for the lentic water used for oviposition (Pearl & Hayes, 2004). As such, elevation, slope, and climate data are variables that are important to predicting suitable locations. Variables that can capture these aspects of Oregon spotted frog will benefit the model's predictive ability and are included as the key inputs in this study.

One of the main uses of Maxent is to locate areas of suitable habitat to guide survey efforts for less documented species (Blank & Blaustein, 2012). Applying Maxent in this way to model Oregon spotted frog breeding habitat in the entire Chehalis Basin could provide locations that may have frogs but have not been previously documented. However, many of the wetlands in the floodplain and off-channel habitats in the main stem of the Chehalis River have been surveyed, which allows for an additional use for the Maxent model. If survey locations coincide with the model output, it can be assumed that they are suitable breeding habitat, however, none of the surveys detected Oregon spotted frog (M. Hayes, personal communication). Even with this discrepancy, this can be useful as the habitat of the survey sites can be compared with the habitat of known breeding locations to test for differences. A comparison in this manner will also allow for the inclusion of additional variables such as the abundance of invasive species, specifically bullfrogs and exotic fish. Because, biotic influences can determine a species dispersal beyond the abiotic factors, and the Maxent model is only using abiotic variables yet predicting suitable habitat, the presence of these invasive species may be influencing the presence of Oregon spotted frog (Elith & Leathwick, 2009).

METHODS

Oregon spotted frog were not known to occur in the Chehalis Basin until 1990, when they were discovered at Dempsey Creek, a tributary of the Black River (McAllister et al., 1993). Several additional populations have been discovered in the Black River in the years following this initial find. Frogs may have occurred beyond the Black River watershed in the main stem of the Chehalis River floodplain or in its other tributaries. However, surveys in the Chehalis River floodplain have failed to detect Oregon spotted frog. To better understand this apparent absence, Maxent was used to model Oregon spotted frog breeding habitat in the Chehalis Basin, specifically to see if suitable habitat exists elsewhere in the Chehalis Watershed that has the same characteristics of known Oregon spotted frog sites in the Black River. A Maxent species distribution model was developed from the habitat and climatic data associated with extant Oregon spotted frog populations in the Black River watershed. The outputs of the Maxent model revealed that sites surveyed in the Chehalis River mainstem floodplain were predicted to be suitable habitat. The structure and climatic conditions of these sites were compared to the known breeding locations for Oregon spotted frog in the Black River. An additional variable set was evaluated for these locations: the abundance of centrarchid fishes and bullfrogs, exotic species known to be detrimental to Oregon spotted frog. The purpose of this addition was to assess if these exotic species could be limiting Oregon spotted frog distribution in the Chehalis River mainstem floodplain.

Maxent

Maxent is a species distribution model that estimates the probability of presence based on an index of habitat suitability across a targeted geographic area (Phillips et al., 2006). Habitat suitability is defined by the environmental conditions at locations of known occurrence. Occurrence locations are inputted as presence points and environmental data are inputted as raster grid layers that encompass the entire study area, with each cell of the grid being assigned a value of that variable (Phillips, 2017). For example, each cell of a raster layer for slope at a 30-meter resolution would contain a value for the degree of slope found in that 30 m^2. The slope value for a presence point is based off of what cell the point occurs in. Habitat suitability is determined by a value calculated from a set of mathematical transformations, called features. Features are performed on and between the set of environmental values at each presence point, as well as a set of background points randomly selected from the study area (Phillips et al., 2006; Phillips & Dudík, 2008). How much the means of the features at the background points differ from the means of the presence points determines the level of habitat suitability. A habitat suitability index is created that defines the range of values and their level of suitability (Elith et al., 2011). This process is described as model training , as the model is being trained to identify suitable habitat based on the presence points. (Phillips et al., 2006; Phillips & Dudík, 2008). The final Maxent output is the probability of presence of each cell in the raster grid according to the suitability index. Cells that have habitat suitability values close to those of the presence points are deemed to have a high probability of presence while cells that differ substantially from the presence points have a low probability of presence (Elith et al., 2011; Phillips et al., 2017).

Presence Point Selection

To model Oregon spotted frog breeding habitat, egg mass locations were acquired from the Washington State Department of Fish and Wildlife's Priority Habitat and Species database (Washington Deptartment of Fish and Wildlife, 2020). This database includes locations of sensitive species and their associated habitats across the state of Washington. Data points from the Black River were acquired and filtered to include only locations of egg masses collected with GPS during annual egg mass surveys. This filter was applied to avoid including points that might represent dispersal of juveniles, or other conditions and might represent non-representative habitat that was not regularly occupied. In the dataset, the locations of egg mass points were representative of breeding habitat, and confidence was high that these points were accessible to non-breeding habitat. Other points in the dataset were classified as occurrences when individual frogs were observed, however, the context of these observations was uncertain, therefore they were excluded to focus the model on breeding habitat. Since the Oregon spotted frog was discovered in the Black River in 1990, subsequent populations in the watershed have been discovered at various times in the following years (Hallock, 2013; McAllister et al., 1993). Therefore, the data obtained from the WDFW database spans the years 1996 to 2019, with some populations having been sampled multiple times since 1996 and others only recently. Despite this discrepancy, the entire range of surveys years was included for analysis to maximize information on breeding habitat usage. Overall. there were 894 breeding points considered as presence points in the Black River.

Egg masses in the Black River are clustered in distinct groupings of varying sizes. In order to reduce effects from spatial-autocorrelation, points within these groups were spatially filtered using the “Spatially Rarefy Occurrence Data for SDMs” tool in SDMToolbox (Brown et al., 2017). Spatially rarefying points is a process that selects a presence point and then removes every other point within a specified distance (Brown et al., 2017). The objective was to find a spatial distance that balances maximizing information on habitat use (retains a maximum number of points) and keeps the points independent as possible (removes points too close together to be considered independent) (Boria et al., 2014). The points were spatially rarefied to a scale of 300, 400, and 500 meters and the results of each distance were visually compared to gauge the distribution of the remaining points both within and between the original groupings of egg masses. After visually comparing the results, the points remaining at the 500-meter rarified distance were chosen for the model. Because the breeding points occur in distinct groups of varying sizes, the 500-meter distance reduced each group to less than five points, depending on the total area encompassed by the original group. While the groups are not completely independent, as some of the larger groups are represented by multiple points, the remaining points capture the variability of the habitat used in the larger groups. Too much information on habitat use may be lost if all but one point is removed. This process resulted in 29 presence points used for the model (Figure 2). The large reduction in presence points from 894 to 29 avoids overfitting in the final model as the points are concentrated in the Black River, a small portion of the Chehalis Basin. Overfitting can occur when a model is trained from a large number of points in one area, many with non-independent habitat characteristics. The model will overpredict habitat suitability of that small area and fail to generalize predictions to the rest of the study area. Using the minimum number of points to capture the same information lessens this possibility (Boria et al., 2014; Radosavljevic & Anderson, 2014). Maxent is still capable of robust predictions when using a small number of presence points (Pearson et al., 2007). The points were then projected into the WGS 1984 UTM Zone 10 coordinate system and the longitude and latitude were calculated for each point.

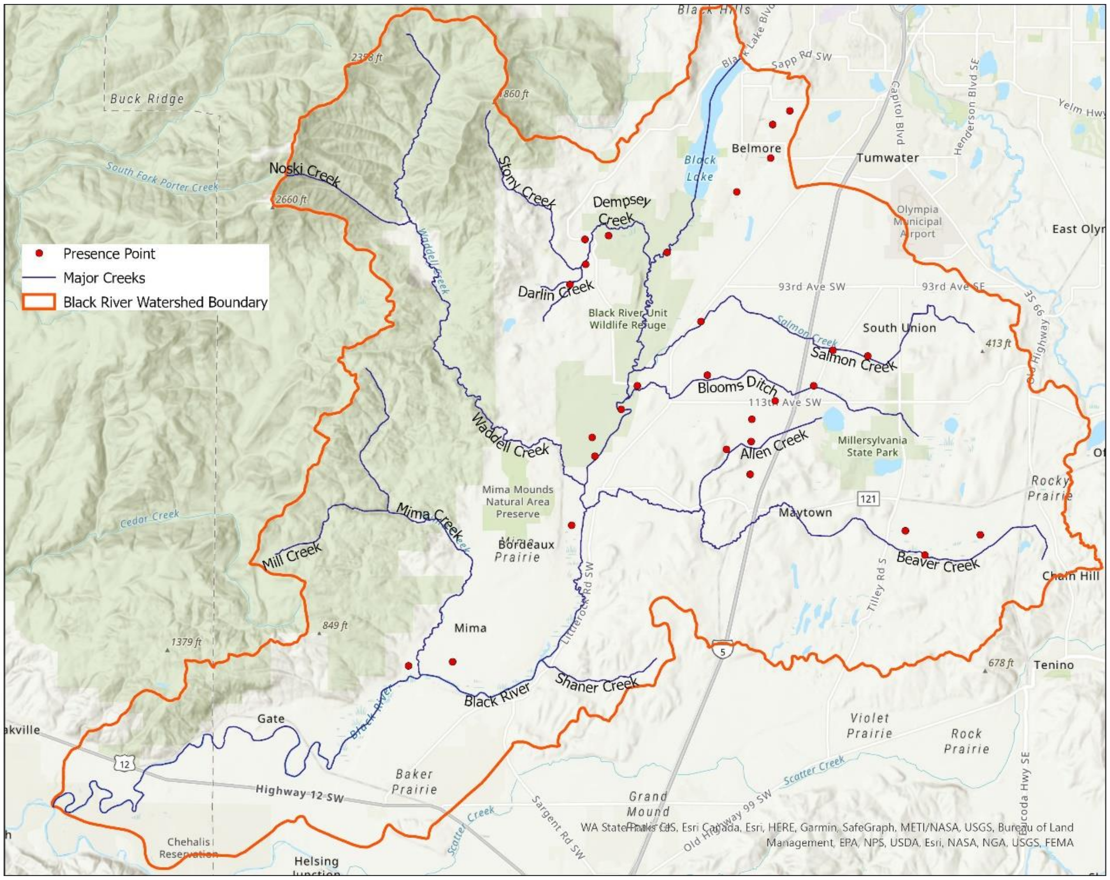

Figure 2. Presence points in the Black River watershed as a result of being spatially rarefied at 500 meters.

Background Point Selection

During the model training process, random background points are selected to compare to the values of the presence points to compute habitat suitability and create a suitability index (Phillips et al., 2006). When selecting background points, Maxent will randomly select points across the study area, therefore the entire range of values from the environmental variables have the potential to be used for training the model. However, if the species is only expected to occur in habitat that is bounded within a limited range of environmental values, a random background point selection can select many points outside of the range of what would be suitable habitat (Merow et al., 2013). The values of many of these points will be far from the values of the presence points, thus biasing the suitability index to be very close to the values of the presence points. The final output will be overfit and predict little probability of presence in cells that are not close in value to the presence points. To increase the predictive ability of the model, it can be beneficial to limit the selection of background points to a spatial range that the species would be expected to disperse, thus limiting the model training to environmental values that are relevant to the species (Merow et al., 2013).

In the case of the Oregon spotted frog, which only occur in aquatic habitat and are limited in their dispersal ability, background points heavily selected from upland habitat would reduce the predictive ability of the model. Therefore, background point selection was limited to a 1.5-kilometer buffer around each of the presence points. This distance was chosen to constrain points to only encompass the breeding site and areas accessible to dispersing Oregon spotted frogs (M. Hayes, personal communication). A "bias file" was created for the modelling software using the "Sample by Buffered Local Adaptive Convex-Hull" tool in SDMToolbox (Brown et al., 2017). The Maxent default of 10,000 background points were used to train the models.

Environmental Variables

Models become more meaningful when the environmental variables are refined and focused on the ecology of the species of interest (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). If too many variables exist in the model, it is difficult to find meaningful relationships between them. In contrast, if too few variables exist, the prediction may be too broad to be useful (Merow et al., 2013). A discerning approach to variable selection in ecological modelling should be adopted and be limited to variables with potential to describe the distribution of the studied species. These can include resource availability, disturbance, and climate. Variables affect species distribution at different scales with resource availability and disturbance describing species distribution at a fine scale, while climate, typically at the resolution measured, tends to be more coarse (Guisan & Thuiller, 2005).

The environmental variables used to model Oregon spotted frog breeding habitat were a collection of raster grids obtained from publicly available sources in a variety of formats and resolutions. Maxent requires variables to be in the same coordinate system and match in resolution and geographic extent. ArcGIS Pro Version 2.7 was used to process variables to meet these requirements and derive new variables from the public data. The variables used in the model were projected into the WGS 1984 UTM Zone 10 coordinate system, resampled to a resolution of 30-meter grid cells if necessary, and clipped to the extent of the Chehalis Basin.

Two sets of variables, structure and climate, were used to create the model for Oregon spotted frog breeding habitat. The structure variables describe the physical environment at a finer scale, while the climate variables generally capture a broader, but local regional scale (Guisan & Thuiller, 2005).

Structure Variables

The structure variables were included based on specific characteristics of Oregon spotted frog breeding habitat. In order to decrease complexity in the model, variables were chosen that are directly related to the ecology, and potentially describe the distribution of the frog. Inclusion of each variable was based on the literature and expert opinions (M. Hayes, personal communication). Table 1 lists the variables collected from public sources and their original resolution.

Table 1. Structure variables used in the Maxent model obtained from publicly available sources and their original resolution.

Variable	Unit	Original Resolution	Source
Digital Elevation Model	Meters	1 arc-sec (~30m²)	National Elevation Dataset (USGS, 2020)
Landcover	Categorical	30 m²	Multi-Resolution Land Characteristics Consortium (Yang et al., 2018)
Open Water			
Developed, Open Space			
Developed, Low Intensity			
Developed, Medium Intensity			
Developed, High Intensity			
Barren Land			
Deciduous Forest			
Evergreen Forest			
Mixed Forest			
Shrub/Scrub			
Herbaceous			
Hay/Pasture			
Cultivated Crops			
Woody Wetlands			
Emergent Herbaceous Wetlands			
Vegetation Height Class	Meters	30 m²	LANDIRE Existing Vegetation (LANDFIRE, 2016b)
Non-Vegetated Classes			
Developed			
Barren			
Quarries/Mines			
Agriculture			
Sparse Vegetation			
Tree Height			
Shrub Height			
Herbaceous Height			
Hydric Soil	Categorical	Vector	WA DNR Geospatial Open Data Portal
Non-hydric			
Hydric			

A digital elevation model was obtained from the United States Geological Service (USGS). Elevation was not directly used as a variable in the final model, but instead was used to create a mask for the structure variables, removing areas from consideration in the model. Cells above 634 meters and below 2.8 meters were removed using the mask. Oregon spotted frog has not been found above 634 meters in Washington state and the 2.8-meter cutoff removes cells below the high tide level in Grays Harbor, removing any marine influence. A slope variable was derived from the digital elevation model using the “Slope” tool in ArcGIS Pro. Oregon spotted frog breed in shallow stable water, found in conjunction with gentle slopes.

The land cover variable defines the dominant cover class of each cell using 20 unique classifications, 15 of which occur within the Chehalis Basin (Yang et al., 2018). Of the excluded classifications, four are unique to Alaska while the only classification of the lower 48 states not found in the Chehalis Basin was perennial ice/snow. The 15 cover classes were reduced to three classes relevant to Oregon spotted frog breeding habitat using the “Reclassify” tool. Reducing the classes to ones relevant to Oregon spotted frog breeding habitat reduces the complexity of the model and removes variables that are not predictive for breeding habitat usage. The new classes were non-habitat, agriculture/pasture, and emergent herbaceous wetland. The classifications were chosen based on the literature, expert opinions and creating a Maxent model only using the landcover variable. The classes in this landcover-only model that were influential in predicting habitat use were kept, while the remaining classes were reclassified into a single “non-habitat” class. An additional variable was derived from the reclassified landcover variable, described as follows: Using the “Euclidian Distance” tool, the proximity of each cell to the nearest emergent wetland or agriculture/pasture cell was calculated. Oregon spotted frog breed in seasonally flooded areas, many of which may extend beyond the boundaries of what was designated as emergent wetland or agriculture/pasture during the image classification process when the cover class variable was created. The proximity variable was meant to capture the movement away from the predictive cover classes if seasonal water levels carried beyond the boundary of the classified cells.

Vegetation height is classified by the dominant vegetation type of each cell (LANDFIRE, 2016a). Similar to landcover, vegetation height was reclassified for relevance to Oregon spotted frog breeding habitat, which consists of short, sparse vegetation. Non-herbaceous vegetation was re-classified as one class and herbaceous heights were classified into 4 categories of 0.2-meter intervals from 0 meters to 0.8 meters. Due to the nature of this classification, this is an ordinal variable, yet it is based on a discrete scale and so run as a continuous variable in the final model (Phillips & Dudík, 2008).

Because of the aquatic nature of Oregon spotted frog, the hydric status of the soil was included. This vector data was obtained from the Washington Department of Natural Resources soil database and converted to raster format using the "Polygon to Raster" tool. The five reconfigured structure variables were included in the final model (Table 4).

Climate Variables

Climate data was obtained from Worldclim as a collection of bioclimatic variables (Table 2). Bioclimatic variables are variations in monthly and annual temperatures and precipitation amounts representing meaningful trends or limiting factors in ecology (Fick & Hijmans, 2017). Trends were calculated based on data collected in the 30-year period between 1970 and 2000 (Fick & Hijmans, 2017). Average solar radiation was obtained for February and March, the period of Oregon spotted frog breeding represented by the presence points.

Table 2. Climate variables used in the Maxent model obtained from Worldclim and their original resolution.

Climatic Variables			
Variable	Unit	Original Resolution	Source
Bioclimatic Variables		30 arc-sec (~1km²)	WorldClim
Annual Mean Temperature			(Fick & Hijmans, 2017)
Mean Diurnal Range			
Isothermality			
Temperature Seasonality			
Max Temp of Warmest Month			
Min Temp of Coldest Month			
Temperature Annual Range			
Mean Temp of Wettest Quarter	°C		
Mean Temp of Driest Quarter			
Mean Temp of Warmest Quarter			
Mean Temp of Coldest Quarter			
Annual Precipitation			
Precipitation of Wettest Month			
Precipitation of Driest Month			
Precipitation Seasonality			
Precipitation of Wettest Quarter	mm		
Precipitation of Driest Quarter			
Precipitation of Warmest Quarter			
Precipitation of Coldest Quarter			
Solar radiation February	kJ m^{-2} day^{-1}		
Solar Radiation March			

All climate variables were obtained in an original resolution of 30 arc-sec, covering about 1 square kilometer. To match the resolution of the structure variables, each variable was rescaled to a 30-meter resolution using the “Resample” tool in ArcGIS Pro. The finer resolution (30-meter) was chosen over the coarser (1 kilometer) in order to retain the level of detail in the structure variables. To select the final climate variables, an intermediate model was created containing all 21 climate variables (Table 3). It is sometimes advised to remove correlated variables if they are known to be irrelevant; however, Maxent will remain stable when using correlated variables (Elith et al., 2011). The climatic conditions for Oregon spotted frog are less understood than the structural requirements, therefore all of the variables were included and then chosen for the final model based on their importance to this intermediate model. Maxent grades variables on two metrics of their importance to the model, the percent contribution and the permutation importance. Out of the 21 variables in the intermediate model, those with a permutation importance above 5% were chosen for the final model.

Table 3. The percent contribution and permutation importance of all 21 climate variables when run in a Maxent model.

Variable	Percent Contribution	Permutation Importance
Precipitation of Driest Quarter	22.3	20
Precipitation of Wettest Month	18.3	14.9
Solar radiation February	14.1	1.9
Mean Temp of Coldest Quarter	12.5	10.6
Temperature Annual Range	8.8	26
Annual Mean Temperature	8.4	19.9
Mean Temp of Wettest Quarter	3.6	2.6
Precipitation of Warmest Quarter	2.9	0
Min Temp of Coldest Month	2.7	1.4
Precipitation Seasonality	2.7	1.1
Mean Diurnal Range	1.3	0.2
Precipitation of Wettest Quarter	1.2	1.1
Solar Radiation March	0.6	0.2
Precipitation of Driest Month	0.3	0
Isothermality	0.2	0.3
Temperature Seasonality	0	0
Precipitation of Coldest Quarter	0	0
Mean Temp of Warmest Quarter	0	0
Mean Temp of Driest Quarter	0	0
Max Temp of Warmest Month	0	0
Annual Precipitation	0	0

The percent contribution of each variable is calculated by Maxent as it is creating the model (Phillips, 2017). As each variable is included in the algorithm, it increases the training gain. The training gain is a measure of the model's ability to differentiate background points from a presence point (Merow et al., 2013). The model starts as a uniform distribution or maximum entropy, of suitable habitat. As variables are included, they add constraints, which are defined by the values at the presence points, so the distribution beings to shrink. The gain is how much this distribution shrinks around the presence points. As the gain increases with the addition of variables, the model becomes more defined according to the presence points. The percent contribution of each variable is a measure of how much they increase the gain when the model is being created (Phillips, 2017; Phillips et al., 2006).

The permutation importance is defined by the variable's influence on the final model. The area under the receiving operator curve (AUC) is a measure of the model's ability to differentiate between suitable and unsuitable habitat (Merow et al., 2013). To measure the permutation importance of each variable, the values of that variable at each training point are randomly permuted. When these values change, the resulting AUC will change as well (Songer et al., 2012). A decrease in AUC indicates a decrease in the model's predictive ability. The decrease is converted to a percentage and is reported as the permutation importance. A large decrease in AUC indicates that the model is relying heavily on that variable to differentiate suitable and unsuitable habitat (Phillips, 2017). Permutation importance is a better indicator of variable importance to the final model compared to the percent contribution (Songer et al., 2012). There were five climatic variables with a permutation importance above five percent: precipitation of the driest quarter, precipitation of the wettest month, mean temperature of the coldest quarter, temperature annual range, and annual mean temperature. These variables were selected to be used as the climate variables in the Maxent model (Table 4).

Table 4. Final structure and climate variables representing Oregon spotted frog breeding habitat used in the Maxent model.

Structure Variables		
Variable	Unit	Data Type
Slope	Degrees	Continuous
Landcover	Categorical	Categorical
Non-habitat		
Agriculture/Pasture		
Emergent Herbaceous Wetland		
Proximity to Cover Class	Meters	Continuous
Herbaceous Vegetation Height	Meters	Continuous
Non-herbaceous		
0 - 0.2 meters		
0.2 - 0.4 meters		
0.4 - 0.6 meters		
0.6 - 0.8 meters		
Hydric Soil	Categorical	Categorical
Non-hydric		
Hydric		
Climate Variables		
Variable	Unit	Data Type
Precipitation of Driest Quarter	Mm	Continuous
Precipitation of Wettest Month	Mm	Continuous
Mean Temperature of Coldest Quarter	°C	Continuous
Temperature Annual Range	°C	Continuous
Annual Mean Temperature	°C	Continuous

When running the model in Maxent, the options to create response curves and variable jackknives were selected. Response curves chart the probability of presence with the values within each environmental variable, thus displaying the bounds of suitable habitat for each variable (Phillips, 2017). The variable jackknife is an additional indicator of importance of each variable to the model. A model is created with each variable in isolation and the increase in training gain is calculated. A large increase in training gain indicates that the variable has information useful for training the model. An additional model is created by removing each variable and calculating the decrease in training gain. A large decrease means the variable has information that is not found in the other variables (Phillips, 2017).

Modelling

Using Maxent, version 3.4.4 (Phillips et al., 2020), Oregon spotted frog breeding habitat was modelled for the Chehalis Basin. The 29 spatially rarefied points in the Black River, and the 1.5-kilometer buffer around each point were used for the presence points and background point selection bias file. The environmental variables were the five structure variables and five climate variables detailed in Table 4. The default settings in Maxent were used which include 10,000 background points, linear, quadratic, product and hinge features, and a regularization multiplier of 1 (Phillips & Dudík, 2008). The default output format, complimentary log-log (cloglog), was chosen for the final model output (Phillips et al., 2017). This output format displays the probability of presence of each cell based on the estimate of suitable habitat (Phillips et al., 2017).

Model Evaluation

Model evaluation is a critical step to determine the predictive ability of the model when presented with data other than the training data. Commonly, when there are sufficient presence points, a subset of these points is removed to be used as testing data. The training points (the ones left) are used to build the model and the testing points (the ones removed) are used to test the model's ability at determining if they are suitable habitat. The AUC is a common metric of evaluating the model's success at differentiating test points from background points (Merow et al., 2013; Pearson et al., 2007). However, when sample sizes are small (about 25 or less) this method is less robust and a different evaluation approach was developed (Pearson et al., 2007; Shcheglovitova & Anderson, 2013).

When the sample size of the presence points is small, removing a portion of the points for testing may limit the model's predictive ability due to the loss of information from those points.

Therefore, a jackknife, or leave-one-out, approach has been developed for small samples (Pearson et al., 2007). This approach to model evaluation retains all of the presence points as training points, save one. The remaining point is used as the test point. The model is trained with the remaining presence points and then determines the habitat suitability of the testing point. Suitability is determined by a threshold based on the values of the training points. A value greater than the threshold is considered a success and an omission if it is less. The test point is replaced and a new test point is removed from the presence points. This process is repeated for every point (Groff et al., 2014; Pearson et al., 2007). The results of each iteration are compiled and the success and omission rates are calculated for the model. A p-value is computed using pvalueCompute, a software developed by Pearson et al 2007. A significant p-value indicates that the success rate of the model using the testing points is better than randomly using a set of background points (Pearson et al., 2007).

Due to the limited number of samples (n=29) in the Black River, the Maxent model was evaluated using the leave-one-out approach. The model was run 29 times and the success of each iteration at predicting the testing point was evaluated at two different thresholds, the minimum training presence and the 10-percentile training presence. While all are considered suitable habitat, training points are ranked based on their values according to the habitat suitability index created by the model. The thresholds are based on these rankings. The minimum training presence threshold is set at the lowest valued training point (Pearson et al., 2007). If the testing point has a suitability value less than the lowest ranked training value, it is an omission. The threshold for the 10-percentile training presence is set at the lowest ten percent of the training points (Pearson et al., 2007). The significance of the success rate at each threshold was evaluated using the pvalueCompute software developed by Pearson et al 2007.

Watershed Comparison

Chehalis River Survey Point Selection and Comparison Criteria

The purpose of the watershed comparison is to assess the habitat suitability of surveyed sites in the Chehalis River mainstem floodplain based on the habitat conditions of Oregon spotted frog breeding habitat in the Black River. No historical records of Oregon spotted frogs exist in the Chehalis Basin outside of the Black River; survey efforts in the Chehalis River floodplain have not been successful at locating new populations. Using Maxent to model suitable habitat across the Chehalis Basin will allow for the comparison of the habitat characteristics of the Chehalis survey points to those of known Oregon spotted frog breeding locations in the Black River. Differences in these characteristics may provide insight into explaining the presumed absence of the frog in the Chehalis River.

The locations of survey sites in the Chehalis River floodplain were acquired from Washington Department of Fish and Wildlife biologists. Surveys for pond breeding amphibians were conducted from 2013 to 2017 (Holgerson et al., 2019). The survey data was a GIS containing polygons delineating each wetland that was surveyed. The "Feature to Point" tool in ArcGIS was used to generate a point within each survey polygon to represent each survey site. There were 189 survey points.

The Maxent model output predicted the probability of presence of Oregon spotted frog across the Chehalis Basin based on an index of habitat suitability derived from the environmental characteristics of the presence points in the Black River. Survey points selected for comparison were chosen according to a threshold of probability of presence above 0.7. Because the probability of presence is associated with habitat suitability, points selected at a threshold of 0.7 are expected to have moderate to high habitat suitability. The points selected at the 0.7 threshold were then filtered by size and form. Wetlands smaller than 0.4 hectares or classified as creeks were removed. Oregon spotted frog breed in lentic water, therefore survey points in creeks are not suitable as breeding habitat. Points classified as ponds or oxbows were retained for use in the analysis. Frogs also tend to occupy large wetland complexes, therefore survey sites smaller than 0.4 hectares were removed. While still not very large in isolation, many of the sites 0.4 hectares and larger are connected aquatically to others, resulting in larger wetland complexes. Under this assumption, the 0.4-hectare threshold was used to avoid being too restrictive in the selection of survey points. There were 47 survey points that met the filtering criteria, 29 of which were randomly chosen to be compared to the 29 presence points in the Black River (Figure 3).

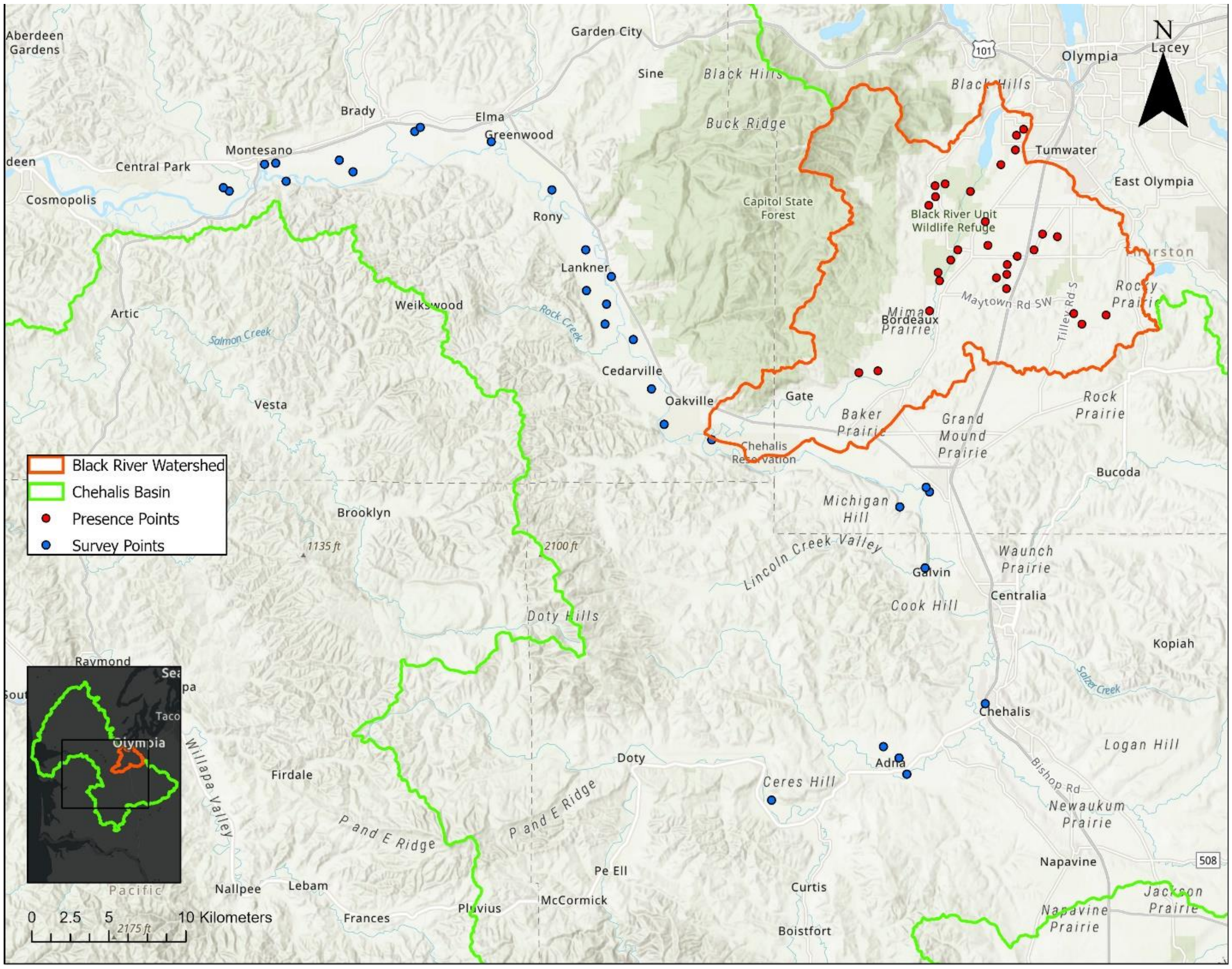

Figure 3. Location of Chehalis River mainstem floodplain survey points and Black River presence points used in the comparison analysis. Survey points were selected based on their predicted probability of presence according to the Maxent model (> 0.7).

At each Chehalis River survey and Black River presence point, the values of the 10 environmental variables used in the Maxent model were obtained using the “Extract Multi Values to Points” tool in ArcGIS Pro. This tool extracts the values of a raster dataset at the specified point. Three additional variables describing the abundance and presence of exotic species (bullfrogs and centrarchid fish species) were included for each survey and presence point. These exotic species are especially detrimental to Oregon spotted frog persistence, and their presence may represent another basis for the absence of frogs outside of the Black River (Holgerson et al., 2019; Pearl et al., 2004). The abundance ranks of centrarchids and bullfrogs were scored as 0, 1, or 2 according to the number of observed individuals at each presence or survey point. The ranks were classified as absent (0, no observations), rare (1, less than 10 observations), and abundant (2, 10 or more observations). The frequency of presence of these species was also included in this comparison. If each point had either a fish or bullfrog occurrence the point was considered occupied by an exotic species.

Following the methods described above, two additional models were created solely for the comparison analysis: a model using only the five structure variables and one using the five climate variables (Appendix 1). The purpose of the variable specific models was to select survey locations for comparison from the Chehalis River mainstem floodplain according to habitat suitability based only on structure or climate. Survey points selected from the structure-only model were compared to the Black River presence points by the five structure variables and the points in the climate-only model were compared by the five climate variables. Both exotic species abundance variables were included for the variable-specific models.

Statistical Analysis

The Black River presence points and Chehalis River survey points were compared by the ten environmental variables (five structure and five climate) used in the Maxent model and two variables describing the abundance of exotic species (centrarchids and bullfrogs). For the continuous and ordinal variables, each was tested for a normal distribution with a Shapiro-Wilk test. If they were normally distributed a two-sample t-test was conducted if the variances were similar and a Welch two sample t-test was conducted if the variances were not. Three variables met the assumption of a normal distribution: annual mean temperature, precipitation of the wettest month and precipitation of the driest quarter, but only the variances of the annual mean temperature were similar. Square root and log-transformations were attempted if the variables were not normally distributed. however, no transformations were successful in creating a normal distribution for any of the remaining continuous variables in either model. As a result, a Mann-Whitney U test was performed on the following variables: mean temperature of the coldest quarter, the temperature annual range, the distance to cover class, herbaceous vegetation height, slope, the abundance of centrarchids, and the abundance of bullfrogs. A Chi-squared test was conducted on the categorical variables: landcover and hydric soil. Significance was established when the p-values was < 0.05. All statistical analysis was conducted using the computing software, R (R Core Team, 2020).

RESULTS

Maxent

A model was created using Maxent to predict the probability of presence of Oregon spotted frog in the greater Chehalis Basin based on habitat suitability defined by the conditions of presence points in the Black River. The habitat of the presence points was defined by ten environmental variables, five of which describe the structure of the habitat and five describe the climate.

Model Evaluation

The Maxent model created for the Chehalis Basin was evaluated using the leave-one-out method. The model had a high predictive ability at both thresholds and was statistically significant compared to a random selection of background points ($p \leq 0.001$) (Table 5). The success rate at the minimum training presence threshold was 93% with an omission rate of 7%. The success rate at the 10-percentile training presence threshold was 83% with an omission rate of 17%.

Table 5. The success rate, omission rate, and associated p-values of the Maxent model developed for the Chehalis Basin. Success was evaluated at two thresholds, the minimum training presence (MTP) and the 10-percentile training presence (10TP).

Maxent Model Evaluation			
Threshold	Success Rate	Omission Rate	p-value
MTP	0.931034	0.068966	0.000
10TP	0.827586	0.172414	0.000

Predicted Distribution

The Maxent model predicted the distribution of suitable breeding habitat for the Oregon spotted frog not only in the Black River, where frogs currently persist, but in the greater Chehalis

Basin as well. Because no records of Oregon spotted frog in the Chehalis Basin exist outside of the Black River watershed, this distribution may potentially be mapping the historic presence of the frog if they ever occurred outside of the Black River. Analysis of the environmental conditions at these locations may reveal factors for their current, presumed absence. The cloglog output format predicts the probability of presence based on habitat suitability. The higher the probability, means the greater the estimate of suitable habitat.

In the Black River watershed, the largest concentration of highly suitable habitat was located along Dempsey Creek, Blooms Ditch, Allen Creek and along the Back River between Blooms Ditch and Waddell Creek (Figure 4). Moderate to high, but more dispersed, habitat was predicted along Salmon Creek, Beaver Creek and the southern stretches of the river between Shaner Creek and Mima Creek. Additional moderate habitat was predicted at the southern point of Black Lake, the source of the Black River and west of Offutt Lake on the eastern edge of the watershed. Much of the predicted habitat occurred around the presence points and was not distributed into many areas not already known to have frogs.

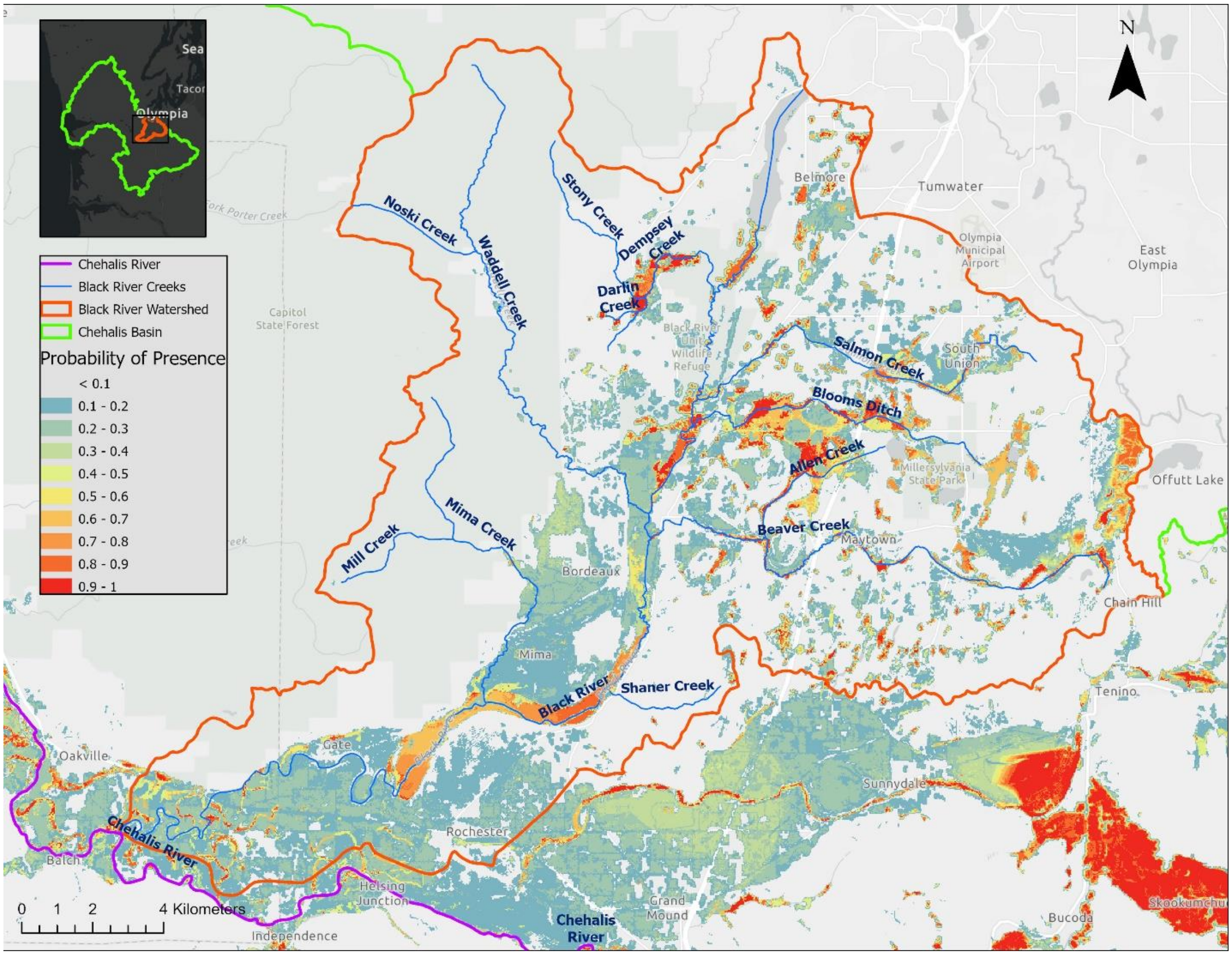

Figure 4. Suitable breeding habitat for the Oregon spotted frog in the Black River watershed according to the Maxent model. The warmer colors represent an increased probability of presence based on the estimate habitat suitability.

The highest concentration and highest probability of presence in the entire Chehalis Basin occurred in the tributaries flowing into the Chehalis River in the upper reaches of the watershed (Figure 5). The Skookumchuck River, Hanaford Creek, Salzer creek and the Newakum River were all predicted to contain highly suitable habitat. Much of the habitat along these tributaries moving eastwards from the Chehalis River have a probability of presence above 0.8. Additional moderate suitable habitat was found along Lincoln and Bunker Creeks, tributaries on the west side of the Chehalis River. In the upper Chehalis Basin, little suitable habitat was predicted along the Chehalis River itself, other than at the confluences of the eastern tributaries. However, this trend changes moving down river into the lower reaches of the watershed.

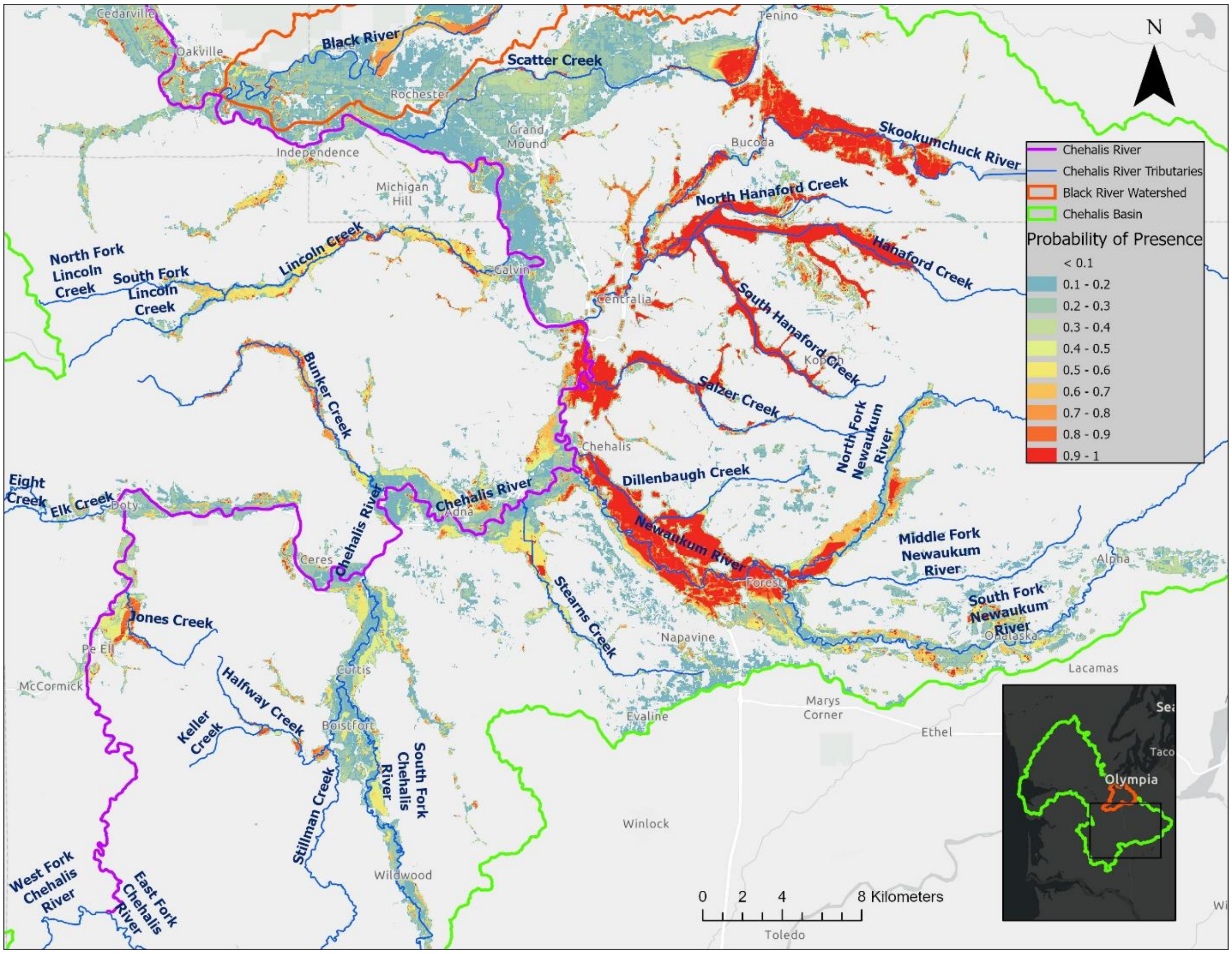

Figure 5. Suitable breeding habitat for the Oregon spotted frog in the Upper Chehalis River Basin. The warmer colors represent an increased probability of presence based on the estimated habitat suitability.

Suitable habitat in the lower Chehalis Basin was confined to the floodplain of the Chehalis River (Figure 6). Most of the highest suitable habitat along this stretch was located among the sloughs, specifically, Wenzel Slough at the confluence of the Satsop River, Metcalf Slough, and the assemblage of sloughs near the mouth of the Chehalis River at Grays Harbor, including Elliot, Mox Chuck and Blue sloughs. Additionally, there was scattered habitat along the Wynoochee and Humptulips Rivers but these were not predicted to have a high probability of presence. Oregon spotted frog prefers large wetland complexes with gentle gradients. In this stretch of the Chehalis River, the tributaries are flowing out of the Olympic Mountains at much higher elevations and steeper slopes, thus diminishing the available habitat.

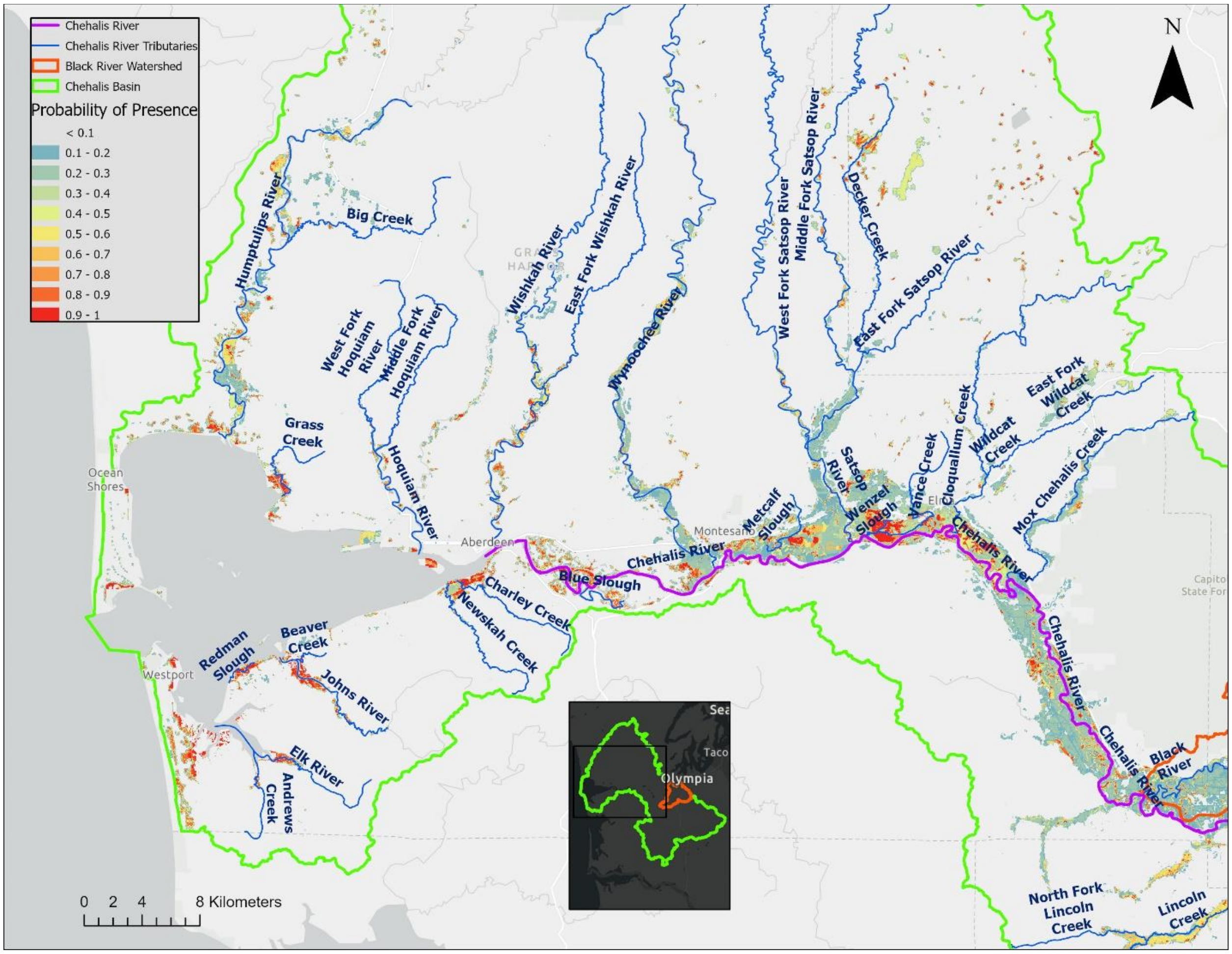

Figure 6. Suitable breeding habitat for the Oregon spotted frog in the Lower Chehalis River Basin. The warmer colors represent an increased probability of presence based on the estimate habitat suitability.

Environmental Variable Importance

Maxent evaluates the importance of variables to the model in multiple ways: the percent contribution of each variable as the model is being trained (percent contribution), the importance of each variable to the final model's predictive ability (permutation importance), and how the variability within each variable defines habitat suitability and the resulting probability of presence (response curves). The evaluation of variables can describe the influence they have on the distribution and ecology of the species, yet they should be considered with caution. The importance of the variable may reflect the Maxent algorithm and not necessarily the preferences of the species.

The distance to cover class variable contributed the most to the Maxent model with a permutation importance of 65% and a percent contribution of 35.8%. This variable contributed the most to the training gain when creating the model and is highly relied upon for the final model's predictive ability. The hydric soil variable contributes substantially less to the final model's predictive ability with a permutation importance of 14.9%; however, it had a high contribution to the training gain with a 27.5 percent contribution. Landcover had a similar percent contribution to hydric soil with 27.9%, however it only has a permutation importance of 3.4%. Slope has the third highest permutation importance, but it is only marginal at 5.4% and only a 2.4 percent contribution. The herbaceous vegetation height and all of the climate variables have a permutation importance and percent contribution value less than 5%. These include: mean temperature of the coldest month, precipitation of the wettest month, annual mean temperature, temperature annual range, and precipitation of the driest quarter. Precipitation of the driest quarter has a permutation importance and percent contribution of 0 percent (Table 6).

Table 6. The permutation importance and percent contribution importance of the environmental variables in the Maxent model.

Permutation Importance and Percent Contribution of Variables to Maxent Model		
Variable	Permutation Importance	Percent Contribution
Distance to Cover Class	65	35.8
Hydric Soil	14.9	27.5
Slope	5.4	2.4
Mean Temperature of Coldest Quarter	3.5	1.2
Landcover	3.4	27.9
Precipitation of Wettest Month	3.3	0.8
Annual Mean Temperature	1.8	0.2
Temperature Annual Range	1.6	0.6
Herbaceous Vegetation Height	1	3.5
Precipitation of Driest Quarter	0	0

The importance of the variables to the model are further highlighted in the jackknife analysis (Figure 7). Maxent runs a model with either the variable in isolation (dark blue) or excluded (light blue) and calculates the resulting training gain. The training gain is the measure of how the model defines a presence point against a background point. The higher the training gain, the more defined the model is by the presence points and is thus better able to distinguish the habitat characteristics at those points (Merow et al., 2013). When excluded, the distance to cover class variable decreased the training gain the most (light blue bar), indicating that this variable provided the most information on the habitat characteristics of the presence points that is not found in the other variables. Hydric soil decreased the training gain second to distance to cover class when it was excluded from the model. These two variables have information pertaining to the presence points that was not found in the other variables. Their high permutation importance further supports this.

When each variable was run in isolation, landcover increased the training gain the most (dark blue bar). By itself, landcover was better able to define the habitat characteristics of the presence points compared to the other variables. When run in isolation, the set of structure variables generally were better able to define the presence points compared the climate variables, which perform poorly in terms of training gain when they were run by themselves.

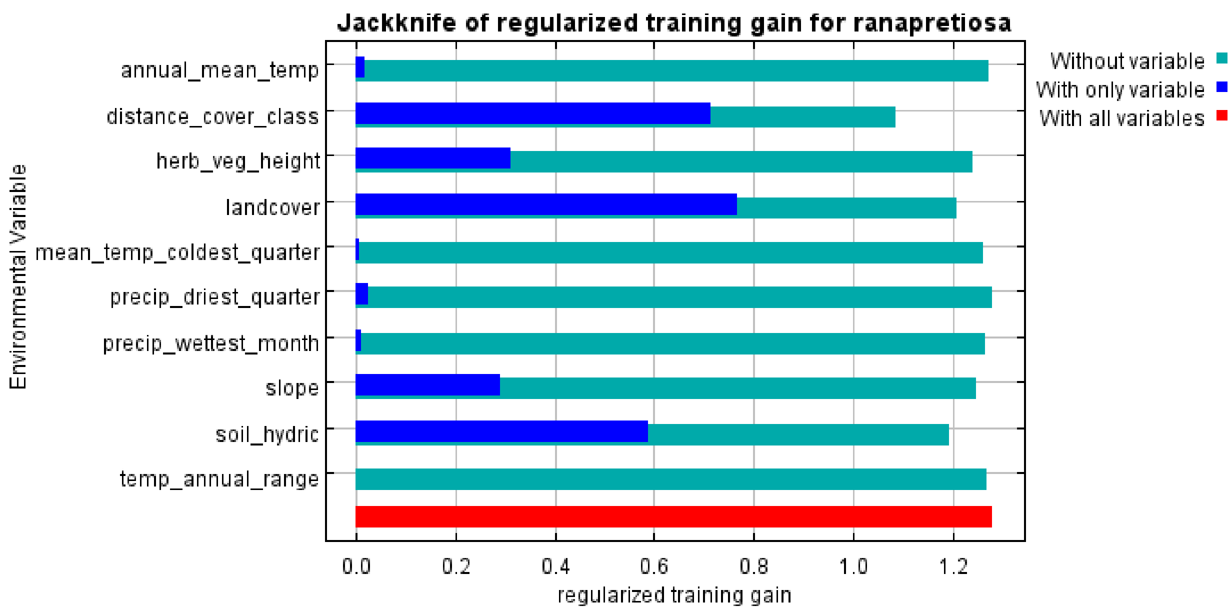

Figure 7. Jackknife analysis of the Maxent variables. The light blue bars measure the training gain of the model when that variable is excluded. The dark blue bars measure the training gain when that variable is run in isolation.

The variable response curves identified the range of values within the variables and how they contributed to the probability of presence in the Maxent model output. The probability of Orgon spotted frog presence favored aquatic conditions and gentle gradients (Figure 8). Probability increases as the distance to the preferred cover class decreases and becomes likely (>50% probability of presence) at less than 15 meters (Figure 8a). The probability of presence was highest among herbaceous vegetation taller than 0.2 meters, and probability increased until the maximum vegetation height of 0.8 meters was reached, which was the tallest height in the data (Figure 8e). While there was not a clear trend between the height classes, the probability of presence was higher in every class compared to the non-herbaceous vegetation class. Although the probability of presence was 40% in the agriculture cover class, probability increased to over 90% when located in the emergent wetland cover class (Figure 8b). Finding Oregon spotted frogs at high slopes was highly improbable but started becoming increasingly probable once slope dropped below 3˚, with a much higher probability at slopes less than 1° (Figure 8c). Soil type was important as well, with an 80% probability of presence within hydric soils (Figure 8d).

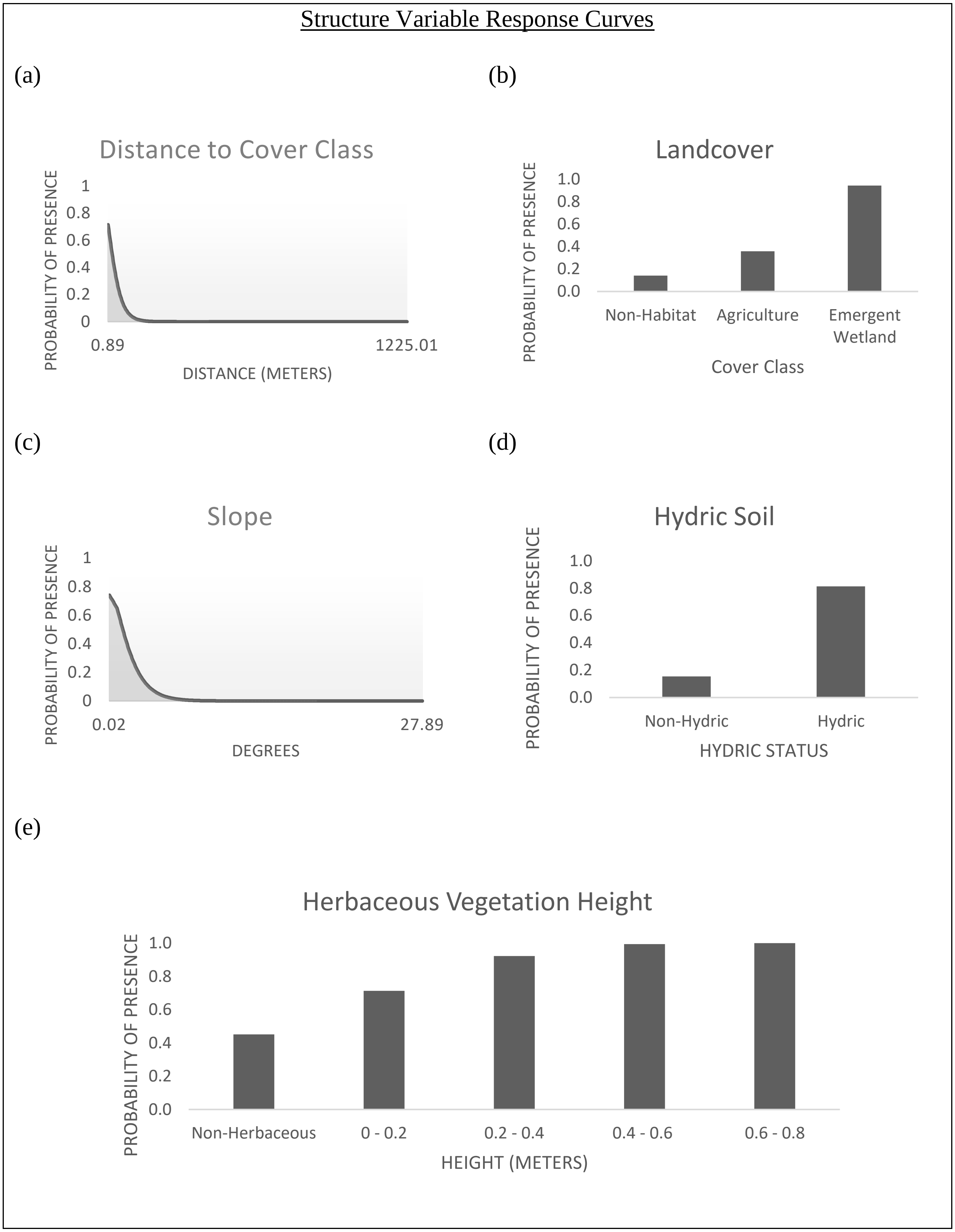

Figure 8. Response curves plotting the probability of presence based on the variation in the structural variables used in the Maxent model. The variables include (a) distance to cover class, (b) landcover, (c) slope, (d) hydric soil status, (e) herbaceous vegetation height.

The probability of presence, according to the climate variables, trended towards increasing probability with warmer and drier conditions (Figure 9). Presence became more likely when the annual mean temperature was greater than 10.15 °C (Figure 9a). Probability increased until the mean temperature of the coldest quarter reached 4.28 °C and then leveled off at 65% (Figure 9b). Probability began to increase as the temperature annual range began to widen beyond 24.47 °C (Figure 9e). The probability of presence increased with drier conditions. Probability began to decrease as the precipitation of the driest quarter exceeded 91 millimeters and the precipitation of the wettest month exceeded 200 millimeters (Figure 9 c and d).

Climate Variable Response Curves

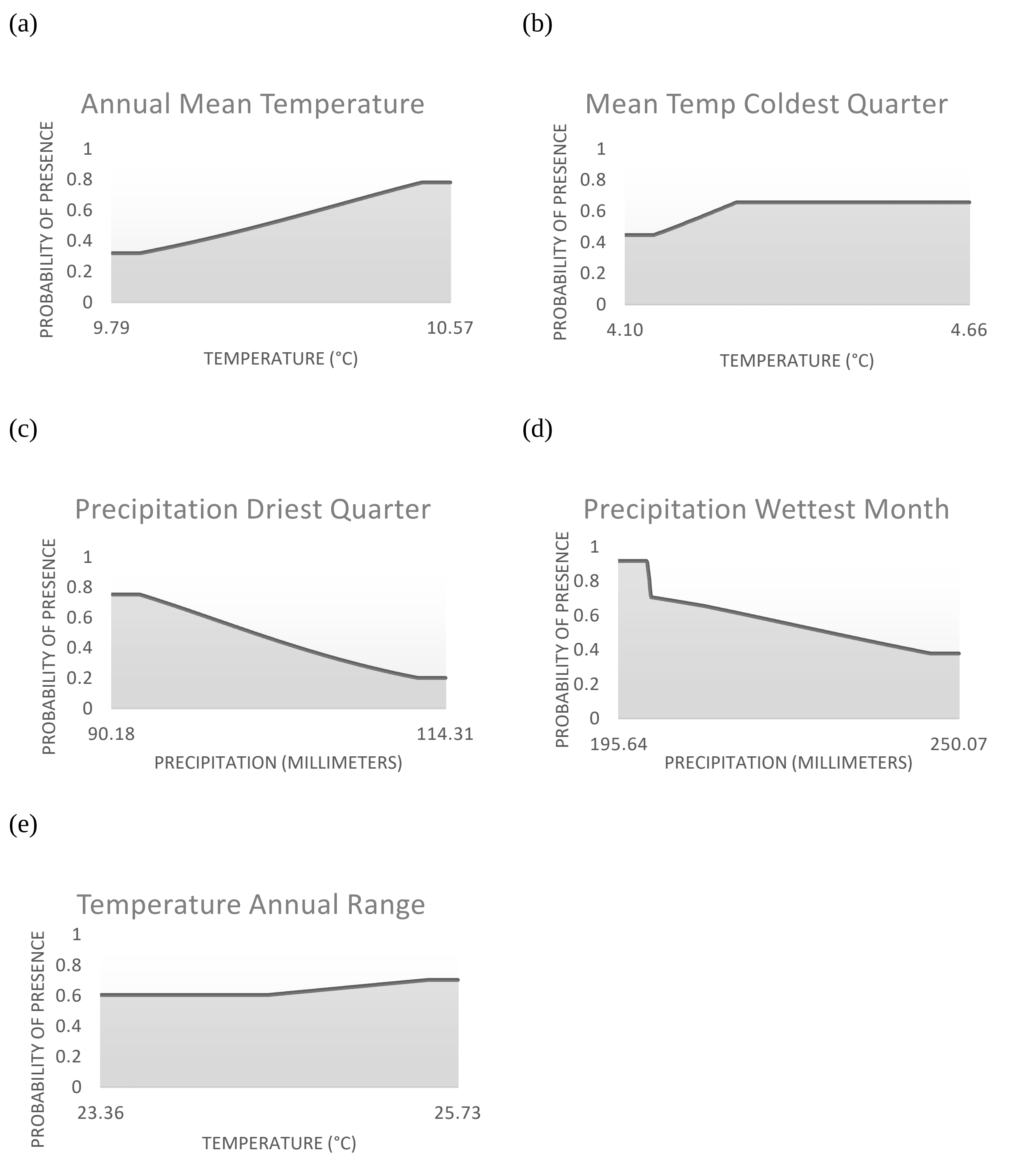

Figure 9. The response curves plotting the probability of presence based on the variation in the climate variables used in the Maxent model. Variables include (a) annual mean temperature, (b) mean temperature coldest quarter, (c) precipitation driest quarter, (d) precipitation wettest month, (e) temperature annual range.

Watershed Comparison

To assess the reason for the apparent absence of Oregon spotted frog in the Chehalis Basin, outside of the Black River, the values of the ten environmental variables used in the Maxent model and the presence and abundance of two exotic species were compared between sites surveyed in the Chehalis River mainstem floodplain to populations in the Black River. The Chehalis survey sites were selected based on moderate to high habitat suitability predicted by the Maxent model.

There was no statistical difference ($p < 0.05$) in the structural variables between points in the Chehalis and points in the Black (Table 7). These variables describe the physical habitat structure and include: the distance to cover class, the herbaceous vegetation height, landcover, slope, and hydric soils (Table 8).

The five climate variables were significantly different ($p < 0.05$) between the rivers (Table 7). The Chehalis points were warmer, wetter and narrower in temperature range compared to the Black (Tables 8). The annual mean temperature was 0.09 °C warmer and the mean temperature of the coldest quarter was 0.53 °C warmer in the Chehalis compared to the Black. There was 50.5 millimeters more precipitation during the wettest month and 24.45 millimeters more precipitation in the driest quarter in the Chehalis compared to the Black. The annual temperature range was 1.42 °C narrower in the Chehalis compared to the Black (Table 9).

The abundance and presence of centrarchids and bullfrogs, were significantly different ($p< 0.05$) between the watersheds (Table 7). The abundance of centrarchids was higher in the Chehalis River floodplain with an average abundance rank of 0.79 compared to 0.10 in the Black. The abundance of bullfrogs was higher in the Chehalis as well with an average abundance rank of 1.59 compared to 0.45 in the Black (Table 8). Exotic species were present at 90 percent of the Chehalis River points compared to 45 percent of the Black River points (Table 8).

Table 7. Results of the comparison analysis of environmental and exotic species variables between the Black River presence points and the Chehalis River floodplain survey points. Significant differences are in bold ($p < 0.001$).

Black River Presence Points and Chehalis River Survey Points Comparison Results				
Variable	Test	df	Statistic	p-value
Structure Variables				
Distance to Cover Class	Mann-Whitney U test		W = 420.5	1.000
Herbaceous Vegetation Height	Mann-Whitney U test		W = 401.5	0.754
Landcover	Chi-squared test	2	X^2 = 4.2125	0.122
Slope	Mann-Whitney U test		W = 444	0.710
Hydric Soil	Chi-squared test	1	X^2 = 0	1.000
Climate Variables				
Annual Mean Temperature	Two Sample t-test	56	t = -3.7316	**0.000**
Mean Temperature of Coldest Quarter	Mann-Whitney U test		W= 0	**0.000**
Precipitation of Wettest Month	Welch Two Sample t-test	29.097	t = -6.8479	**0.000**
Precipitation of Driest Quarter	Welch Two Sample t-test	29.433	t = -9.1964	**0.000**
Temperature Annual Range	Mann-Whitney U test		W = 799	**0.000**
Exotic Species Abundance Variables				
Centrarchid Abundance	Mann-Whitney U test		W = 247.5	**0.001**
Bullfrog Abundance	Mann-Whitney U test		W = 102	**0.000**
Exotic Presence	Mann-Whitney U test		W=609	**0.000**

Table 8. Summary of environmental and exotic species variables used in the comparison analysis between the Black River presence points and the Chehalis River floodplain survey points. Statistical differences are in bold.

Summary Statistics of Black River Presence Points and Chehalis River Survey Points

	Black		Chehalis	
Variable	Mean	St Dev	Mean	St Dev
Structure Variables				
Distance to Cover Class (Meters)	6.21	12.37	6.21	12.37
Herbaceous Vegetation Height (Height Rank)	1.24	1.12	1.38	1.42
Landcover		Categorical		
Slope (Degrees)	0.54	0.57	0.51	0.59
Hydric Soil		Categorical		
Climate Variables				
Annual Mean Temperature (°C)	**10.31**	0.09	**10.41**	0.10
Mean Temperature of Coldest Quarter (°C)	**4.32**	0.09	**4.84**	0.15
Precipitation of Wettest Month (Millimeters)	**212.15**	5.52	**262.74**	39.40
Precipitation of Driest Quarter (mm)	**96.07**	2.26	**120.52**	14.14
Temperature Annual Range (°C)	**24.69**	0.40	**23.26**	0.87
Exotic Species Abundance Variables				
Centrarchid Abundance (Abundance Rank)	**0.10**	0.31	**0.79**	0.90
Bullfrog Abundance (Abundance Rank)	**0.45**	0.51	**1.59**	0.68
Exotic Presence (Percent Occurrence)	**45**	0.51	**90**	0.31

Table 9. The magnitude of change between statistically different variables between the Back River presence points (B) and the Chehalis River floodplain survey points (C).

Magnitude of Change in Statistically Different Variables		
Variables	Difference	Direction
Climate Variables		
Annual Mean Temperature (°C)	0.09 °C	C warmer than B
Mean Temperature of Coldest Quarter (°C)	0.53 °C	C warmer than B
Precipitation of Wettest Month (Millimeters)	50.50 mm	C wetter than B
Precipitation of Driest Quarter (Millimeters)	24.45 mm	C wetter than B
Temperature Annual Range (°C)	1.42 °C	C narrower than B
Exotic Species Abundance Variables		
Centrarchid Abundance (Abundance Rank)	0.69	C more abundant than B
Bullfrog Abundance (Abundance Rank)	1.14	C more abundant than B
Exotic Presence (Percent Occurrence)	45%	C more occurrences than B

The categorical variables, landcover class and soil hydric status, were independent of the watershed the points occurred in. The frequency of points classified as each landcover class was not statistically different between the Black and Chehalis (Table 10). The emergent wetland landcover class had the highest frequency of points with 17 in the Black and 22 in the Chehalis. There were six points in the Black River classified as agriculture but only one in the Chehalis. However, there were six points in both the Black River and the Chehalis River floodplain classified as non-habitat (Table 10a). The frequency of non-hydric and hydric soils at the Black River and Chehalis points was the same (Table 10b).

Table 10. Contingency tables for (a) landcover and (b) hydric soils, the categorical variables used in the Maxent model.

(a)

Landcover Class Frequency	Black	Chehalis
Non-habitat	6	6
Agriculture	6	1
Emergent Wetland	17	22

(b)

Hydric Soil Frequency	Black	Chehalis
Non-Hydric	6	6
Hydric	23	23

Exotic species were more prevalent and abundant in the Chehalis watershed. The abundance of centrarchids at the Chehalis River floodplain survey points were ranked as rare and abundant more often than the Black River presence points, which were more often ranked as absent (Figure 10). The abundance ranks of bullfrogs at the Chehalis River points were more often ranked as abundant, while the Black River points were more often ranked as absent or rare (Figure 11).

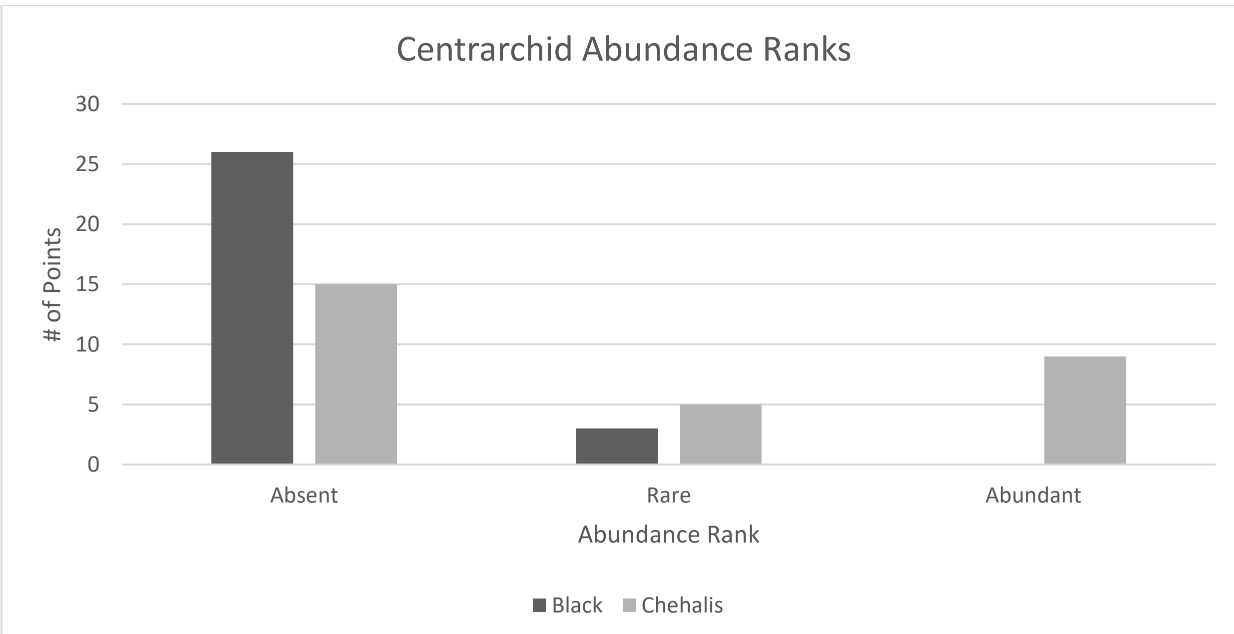

Figure 10. The frequency of abundance ranks of centrarchid fishes at the Black River presence points and Chehalis River floodplain survey points.

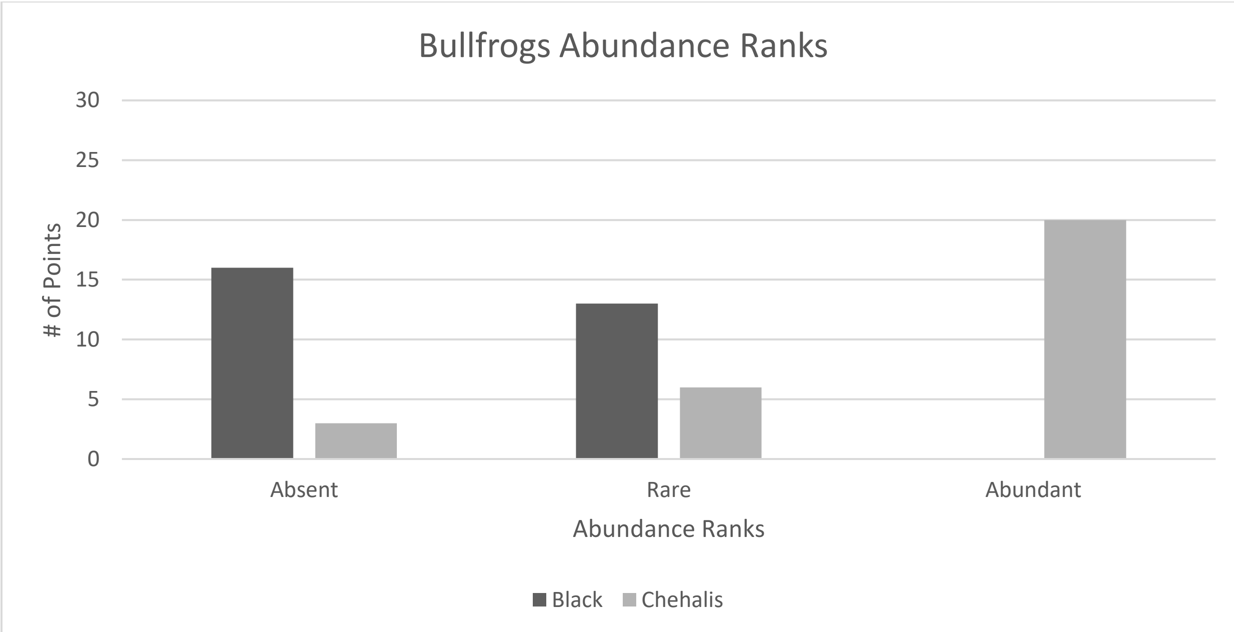

Figure 11. The frequency of abundance ranks of bullfrogs in the Black River presence points and Chehalis River floodplain survey points.

When survey sites were selected from the structure-only and climate-only models, and their respective variables were compared, the results were the same. There was no statistical difference between the structure variables at the structure-only points and the Black River points. There was a significant difference between the climate variables at the climate-only selected survey points and the Black River presence points. The abundance of exotic species was statistically different between the Chehalis River points in both models when compared to the Black River points (Appendix).

DISCUSSION

The Oregon spotted frog, is a federally threatened, and Washington state endangered species due to a large reduction in historical range. As such, one of the recovery objectives is to locate additional populations to increase the current knowledge of the frog's distribution (Hallock, 2013). There are six watersheds in Washington that are currently known to have populations of Oregon spotted frog, one of which, the Black River, is a tributary of the Chehalis River. Due to the aquatic connectivity of the Black and Chehalis rivers, it could be likely that the frogs occupy additional watersheds in the Chehalis Basin, however no records of occurrences outside of the Black River have been documented. To determine potential causes for the absence of Oregon spotted frog from the Chehalis Basin, a Maxent model was created to predict the distribution of suitable habit. That model was based off the habitat of known frog breeding locations in the Black River, and therefore similar conditions were modelled in the rest of the basin. Using this habitat distribution as a selection guide, previous survey sites in the Chehalis River mainstem floodplain were chosen that met a moderate to high level of suitability according to the habitat conditions of known breeding locations. Although these sites were predicted to have habitat characteristics similar to the occupied locations, all surveys in the Chehalis River floodplain have thus far been unsuccessful at locating Oregon spotted frog. The apparent absence of frogs at these sites is consistent with the historical records, as no frogs have been reported in the Chehalis Basin, except in the Black River watershed, which were not discovered until 1990. It can be hypothesized that frogs did once occur in parts of the greater Chehalis Basin, yet by the time they had been discovered in the Black River in 1990, conditions in the remainder of the basin may have been altered to their detriment and eventual extirpation. Therefore, after using the Maxent model to identify locations that are predicted to have similar habitat in the Chehalis Basin, a comparison between the survey points in the Chehalis River floodplain found within habitat considered to be suitable and presence points in the Black River may offer insights as to how these conditions may differ between the Black and Chehalis Rivers. The locations were compared by three criteria: the habitat structure, the climate, and the abundance of exotic species. According to this comparison, habitat structure does not appear to be a limiting factor, yet the climate and abundance of exotic species differ between the two rivers.

The Maxent distribution of suitable habitat extended well beyond the boundary of the Black River watershed, despite no records of Oregon spotted frog occurring elsewhere in the Chehalis Basin. This output may therefore serve as a historical distribution of frogs in the Chehalis Basin, if they ever occurred outside of the Black River. According to the model evaluation, the Maxent model had a high predictive ability at the minimum training presence threshold and a moderately high ability at the 10-percentile training presence threshold with a success rate of 93% and 83% respectively. When determining the importance of the environmental variables, the structure variables contributed the most to the model in both permutation importance and percent contribution. Therefore, the model output is being driven mainly by the conditions of the habitat structure of the Black River presence points and predicted sites across the rest of the Chehalis Basin can be expected to have similar structure based on the variables provided. Indeed, the structure variables at the Chehalis River floodplain survey points and the Black River presence points were not statistically different according to the comparison analysis. This holds true in the complete model as well as the survey points selected for the structure-only model (Appendix).

Although there was not a statistical difference between the structural variables across the basin, it is worth discussing whether the desirable habitat structure is consistent with that presented in the literature for Oregon spotted frog. Probability was highest when points were located within or near emergent wetlands, the preferred habitat types for Oregon spotted frog (Watson et al., 2003). Emergent wetlands provide the appropriate hydrology and vegetation structure needed for the diverse, seasonal habitat requirement of the frog (Watson et al., 2003). While habitat requirements for the frog may differ between season and life cycle stage, all must be aquatic and the Maxent model predicted a higher probability of presence within hydric soils. Hydric soils are formed under anaerobic conditions due to permanent water or seasonal flooding and therefore an indicator of aquatic conditions (Ecology, 1997). Frogs breed in seasonally flooded, shallow areas and reside in permanent water in the non-breeding season; therefore, this prediction is consistent with the frog's lifecycle. The seasonal flooding of Oregon spotted frog breeding habitat may extend beyond the boundary of what is classified as emergent wetland in the data, however, the probability of presence decreases when the distance increases away from the preferred cover classes. Presence is most likely when within the preferred cover class or vey near it.

The vegetation height variable, while less clear in determining the preference of the frog, still makes an important distinction between vegetation type. Oregon spotted frog breed among short-statured and sparse herbaceous vegetation and avoid wooded areas or areas with dense cover (Watson et al., 2003). The model predicted a high likelihood of presence at most of the herbaceous height classes and was less likely when located in the non-herbaceous vegetation class. The preference for frogs is to breed among short vegetation, yet the model predicted suitable habitat at every height class up to one meter, the highest height class in the data. This discrepancy could be a result of the data itself. The vegetation height data describes the dominant vegetation type and height of each 30 square meter cell of the raster layer, yet there is opportunity for variation in heights of each cell (LANDFIRE, 2016a). For example, a cell designated as being dominated by 0.8-meter-tall herbaceous vegetation may still have sufficient areas with variation in height to provide plenty of microsites for breeding habitat. What is significant about the prediction within this variable is that cells designated as non-herbaceous vegetation had a low probability of presence compared to cells classified as herbaceous vegetation. While the exact vegetation height may be lost in the data, the vegetation type is consistent with the preference found in the literature.

Confidence should be high that the model is predicting suitable habitat structure for Oregon spotted frog in the Chehalis Basin. According to the permutation importance of the variables and the model evaluation, the model relied on structure variables the most for its prediction and had a moderately high success rate at detecting test points as suitable habitat. Additionally, the probability of presence increased within the values of each structure variable to mimic the habitat requirements recorded in the literature. Finally, there was no statistical difference between the Chehalis and Black River structure variables. However, despite the predicted availability of structural habitat, there are no occurrences of frogs in the Chehalis Basin and consideration of the structure variables is therefore needed.

Oregon spotted frog have very specific requirements for suitable breeding habitat and while the structure variables were chosen for the model in an attempt to emulate these ecological needs, there are aspects difficult to capture in a way that can be incorporated into the Maxent model, specifically the hydrology. The need for seasonally inundated shallow, lentic water at breeding sites is a critical determinant for Oregon spotted frog (Watson et al., 2003). However, modelling the variability of seasonal inundation on a site-by-site basis, as well as a year-by-year basis can be a challenge for reliable predictions. Besides the variability of the natural hydrology, the level of land use alteration, including the channeling of waterways and habitat conversion to agriculture and urban areas may be markedly different between the Chehalis and the Black River watersheds. The Black River contains one of the largest intact emergent wetland system in the Puget Sound, while the wetlands of the Skookumchuck and Newakum Rivers, Chehalis River tributaries predicted to be highly suitable habitat, have been reduced by up to 75 percent (Species Restoration Plan Steering Committee, 2019). Increased development and agriculture can result in the channeling of waterways for wetland conversion and flood mitigation, which occurs frequently in stretches of the Chehalis River (Ecology, 2016; McAllister & Leonard, 1997). Additionally, the invasion of reed canary grass and the subsequent alteration of the vegetation structure of many wetlands, creates a situation where Oregon spotted frog is reliant on microsites found in opportune openings in the grass (Hallock, 2013; Kapust et al., 2012). The landcover and vegetation data used in the model was classified by vegetation systems and not individual species. Therefore, areas classified as emergent freshwater wetlands, the highest predictive land cover class, may be infested with reed canary grass across the entire basin and the number of microsites available to the frogs can be highly variable between locations. While the Maxent model was highly predictive using the variables provided for the model, individual site visits will be necessary to validate the suitability for Oregon spotted frog. Despite the discrepancies between the data and what may actually be available for Oregon spotted frog, the model predicted suitable habitat at wetlands that were independently surveyed by Washington Department of Fish and Wildlife biologists and determined to be suitable habitat. Even with the field validation of these sites by biologists, Oregon spotted frog was not observed in these wetlands and their absence may be explained by factors other than habitat structure.

According to the comparison analysis, the climate of the Chehalis River floodplain survey points is statistically different than the Black River presence points. The Chehalis River points were wetter and warmer than the Black, yet the Maxent model predicts a higher probability of presence when the climate is warmer and drier. The annual mean temperature of the Chehalis Basin follows an elevational gradient and decreases as elevation increases (Appendix 13a). The higher temperatures are located along the Chehalis River valley and lower elevations of the tributaries matching much of the distribution of predicted suitable habitat from the Maxent model. While they are statistically different, the variation in the average annual mean temperature between the Chehalis and Black River points is only 0.09 degrees C. According to the response curves, the probability of presence is highest when the temperature is above 10 degrees C and both the Chehalis and Black River points have a mean temperature higher than this value. In contrast to the annual mean temperature, the temperature annual range follows an east-west gradient and narrows as the Chehalis River flows westwards to the coast, resulting in the mean temperature of the coldest quarter becoming warmer along the coast than the eastern portion of the Basin, where the Black River is located (Appendix 13b and c). The narrower temperature range provides a more moderated climate condition therefore, a warmer winter on the coast than inland. Similar to the annual mean temperature, while the survey and presence points are statistically different, the means of the temperature annual range and mean temperature of the coldest quarter only vary by 1.42 and 0.53 °C. The temperature variables are statistically different but they are not necessarily inhospitable to frogs. Based on the range of Oregon spotted frog, this variation does not seem likely to be responsible for the absence of frogs in the Chehalis River floodplain as frogs survive in more extreme climates within their range. For example, the winter temperatures at Conboy Lake, the largest remaining population of Oregon spotted frog, regularly reaches temperatures below freezing (Hayes et al., 2001). On the other end of the temperature spectrum, frogs prefer warmwater wetlands, occupying summer water temperatures above 20 °C. If the temperature is more moderate closer to the coast, perhaps the water temperature does not get warm enough for frogs (Hayes, 1994). As long as there is permanent water available throughout the dry season, frogs may be able to persist in warmer climates.

The precipitation in the Chehalis Basin follows an east-west gradient with less rainfall during both the wettest month and the driest quarter occurring in the eastern portion of the basin (Appendix 13d and e). Oregon spotted frog is completely aquatic, yet the Maxent model predicts the highest amount of suitable habitat in the driest tributaries. Granted, this prediction is most likely based off of the habitat structure of these tributaries as the precipitation of the driest quarter had zero percent contribution and permutation importance and the precipitation of the wettest month had a permutation importance of only 3.3 and a percent contribution of 0.8.

Where climate may have an influence, but is missing from the model, is the effect on water temperatures. The elevation of the headwaters of the tributaries may have an effect on water temperatures, which could be a limiting factor for Oregon spotted frog, which use warmwater habitat. Typically, frogs inhabit wetlands with water temperatures that exceed 20 °C during the summer months (Hayes, 1994). The Black River originates from Black Lake at a low elevation and remains so for its entire length before meeting the Chehalis River. The river is exposed to the warmer, low elevation temperatures for its entirety. In contrast, the tributaries in the north of the basin, such as the Wynoochee or Satsop rivers, originate in the Olympic mountains, where temperatures are colder than the Black River and water temperatures may be influenced by snowmelt as opposed to just rain. Additionally, in the northern tributaries, the mean temperature cools off rapidly when moving north and increasing elevation from the mainstem of the Chehalis River, which exposes greater lengths of the rivers to cooler temperatures. In contrast, the annual mean temperature of the eastern tributaries, such as the Skookumchuck, Newakum, and Black rivers, remains warmer for a greater distance when moving upriver from their confluences at the Chehalis River. Additional data would be needed to evaluate this hypothesis.

It is important to interpret the results of the Maxent model with caution, especially when the variables responsible for the distribution of OSF are not entirely understood. This is especially true for the climate favored by the Oregon spotted frog. Unlike habitat structure, the climate of the Oregon spotted frog is less understood, therefore, variable selection was not ecologically focused, but instead relied on the mathematical side of the relationship between ecology and statistics in species distribution modelling. Predicting the climate of Oregon spotted frog habitat in the Chehalis Basin may be limited by using a presence-only model. Because the model only uses information from known locations and formulates the prediction off of the conditions of these locations, when all of the occurrence samples are located in one end of a spectrum, such as the precipitation gradient in the Chehalis Basin, it is only capable of predicting habitat that falls in the conditions of that end of the spectrum. As a result, greater predictive weight may be placed on the drier conditions of the eastern basin, as that is the conditions of the presence points that the model was trained with. It cannot be said definitively if climate is a limiting factor for Oregon spotted fogs in the Chehalis Basin, however based on this study, the climate outside of the Black River watershed is statistically different and warrants further study.

A climate model that incorporates the climatic conditions of the entire range of Oregon spotted frog may allow for the inclusion of more inputs and better predict the conditions favored by the frog.

Besides climate being a potential limiting factor, the presence of exotic species is another difference between the Black and Chehalis rivers. The greater abundance of exotic fish and bullfrogs in the Chehalis River floodplain may be a direct cause of Oregon spotted frog absence as the presence of these exotic species is associated with a negative abundance of native amphibians (Holgerson et al., 2019). In the Chehalis River floodplain, 90% of the survey points had occurrences of fish, bullfrogs or both compared to the Black River where only 45% of the presence points had occurrences of these species.

The exotic fish of greatest concern are in the Centrarchid family and include species of bass and crappie. These are warmwater fish introduced into many of Washington's rivers for sport fishing (Hallock, 2013). They increase competition and predation on Oregon spotted frog. In the Black River, centrarchids were absent at most of the sites with only a few sites having a rare occurrence. In the Chehalis River floodplain, half of the sites did not have exotic fish but there were many sites with an abundance of occurrences. The difference in abundance of centrarchids between the two rivers was statistically different. As such, presence of the frog may be limited in the Chehalis by the presence of centrarchids.

Almost all of the Chehalis River floodplain sites had some degree of bullfrog occurrence, many of which were abundant. In the Black River, half of the sites did not have bullfrogs and half were rare. In both cases, the abundance of these species was statistically different between the rivers and greater in the Chehalis River.

Centrarchids and bull frogs have been shown to be detrimental to Oregon spotted persistence and if left unmanaged, can cause local extirpations. At Conboy Lake National Wildlife Refuge, when bullfrog management was halted, the populations of Oregon spotted frog began to decline (M. Hayes, personal communication). Bullfrogs share similar habitat with Oregon spotted frog and may be outcompeting for resources and increasing predation (Pearl & Hayes, 2004; Rowe et al., 2021). Exotic fish increase predation pressure on Oregon spotted frog and when they are present in aquatic connectors between populations, especially permanent ones, they can increase isolation and sever genetic exchange (Bradford & Tabatabai, 1993). The abundance of exotic fish is negatively associated with many amphibians native to the Pacific Northwest (Holgerson et al., 2019). Oregon spotted frogs are particularly vulnerable to both of these species due to their aquatic nature as they cannot escape into terrestrial habitat during the non-breeding season (Hayes, 1994).

The exotic abundance data for the Chehalis River floodplain sites was collected at breeding sites as well as non-breeding habitat, while the data from the Black River was collected only during breeding surveys. Surveys of non-breeding habitat in the Black River could inform of their presence in overwintering habitat or in the permanent water habitat used in the warmer months. However, it could be assumed that if frogs are using breeding habitat, the exotics are not overly abundant in non-breeding habitat as they are connected aquatically and would be detrimental to frogs during the remainder of the year. Following this assumption, the non-breeding sites are still likely to have fewer exotics than the Chehalis River or the breeding capability of frogs in the Black River would be greatly diminished. Never the less, locating and documenting the abundance of exotic species in all habitat types can guide conservation and management efforts before the balance shifts too far in favor of exotic species. From what is currently known, the Black River is the only bastion for Oregon spotted frog in the Chehalis Basin, therefore, protecting it from invasive species should be a top conservation goal.

This study was an initial attempt at using a species distribution model to locate potential habitat and asses site differences between occupied and unoccupied sites for the Oregon spotted frog. However, additional variables and a “finer tuned” modelling approach may be necessary to fully understand the absence of the frog in the Chehalis Basin. Because of the aquatic nature of Oregon spotted frog, including variables on the seasonal hydrology, water temperature and water quality may capture barriers to dispersal missing from this study. The Maxent model itself may need adjustment as well. Statistical packages have been developed that guide the user to tune different settings to aid with issues such as correlated variables and over fitting. In certain cases, these methods have been shown to create a better prediction beyond the default settings within Maxent.

The strongest evidence for the presumed absence of Oregon spotted frog in the Chehalis Basin, based on the variables considered in this study, is the presence and abundance of exotic species. According to the model, the structural habitat found in the Black River is available in the Chehalis River and many of its tributaries. While the climate is statistically different between the points in the two rivers, it cannot be said with certainty that there is enough of a difference to explain their absence. However, the abundance of exotics, has a clear distinction between the two rivers and both species have a higher instance of occurrence and abundance in the Chehalis River floodplain compared to the Black River. As these species have been associated with a decrease in Oregon spotted frog presence, this points to a potential factor for their absence in the Chehalis River floodplain. The Black River remains one of the only known rivers in Washington to have populations of Oregon spotted frog because the habitat structure is intact and the presence of invasive species appears to be low enough to allow for their continued persistence. Conserving this remaining habitat and preventing invasive species from establishing to harmful levels needs to be a high priority to preserve this already threatened species.

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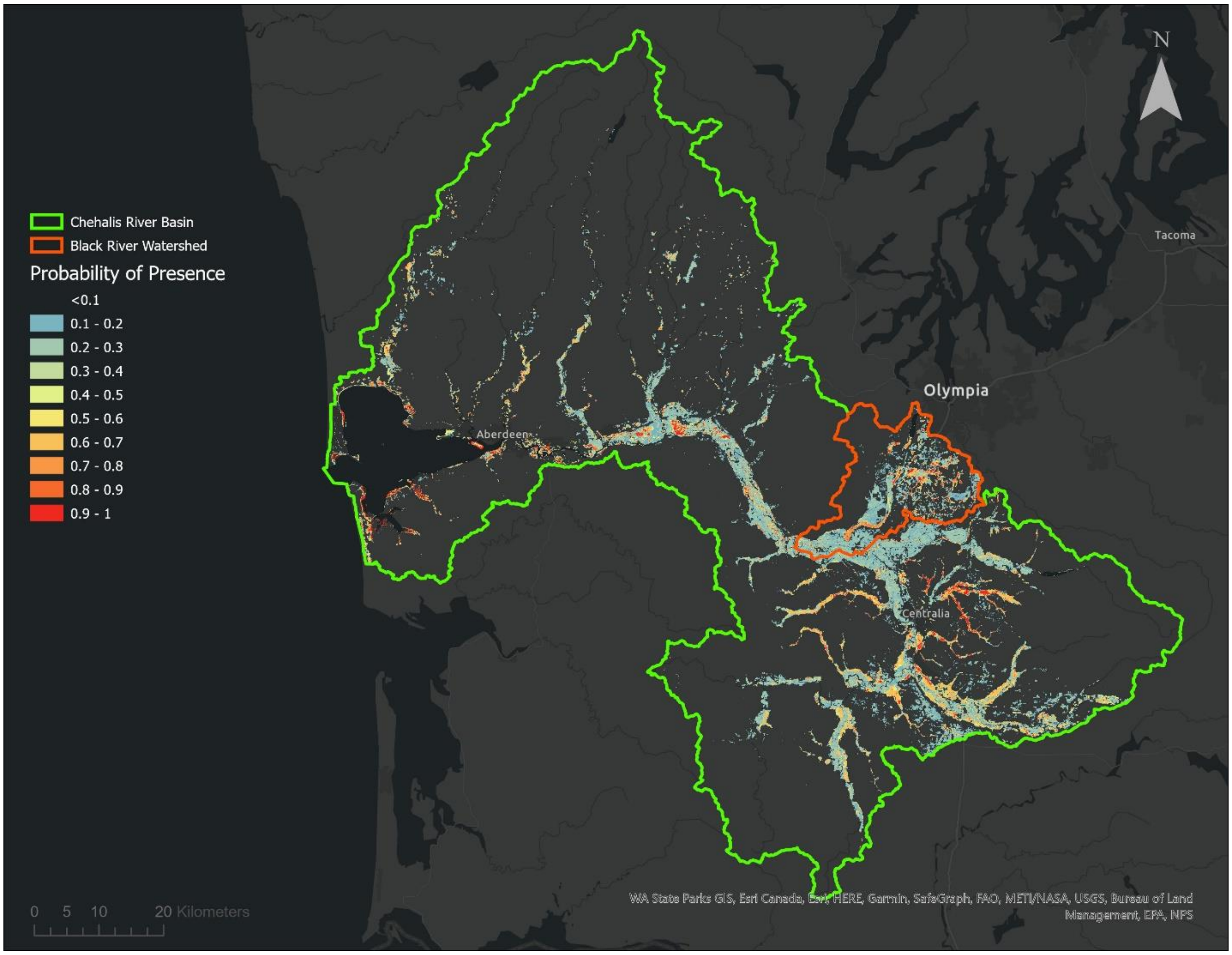
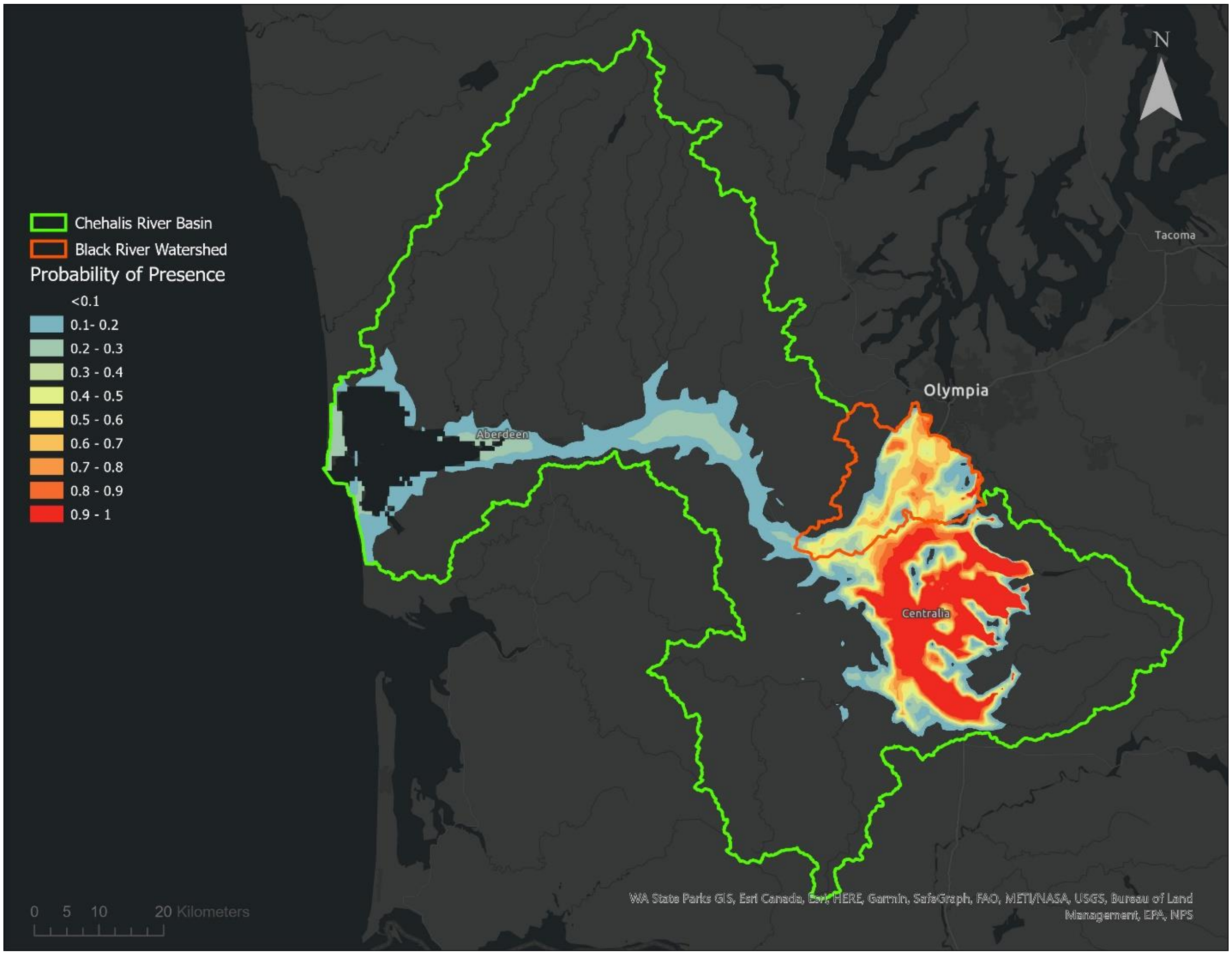
APPENDIX



Appendix 1. Predicted suitable habitat for the Oregon spotted frog in the Chehalis Basin according to the structure variables.



Appendix 2. Predicted suitable habitat for the Oregon spotted frog in the Chehalis Basin according to the climate variables.

Appendix 3. The success rate, omission rate, and associated p-values of the structure-only and climate-only Maxent models developed for the Chehalis Basin. Success was evaluated at two thresholds, the minimum training presence (MTP) and the 10-percentile training presence (10TP).

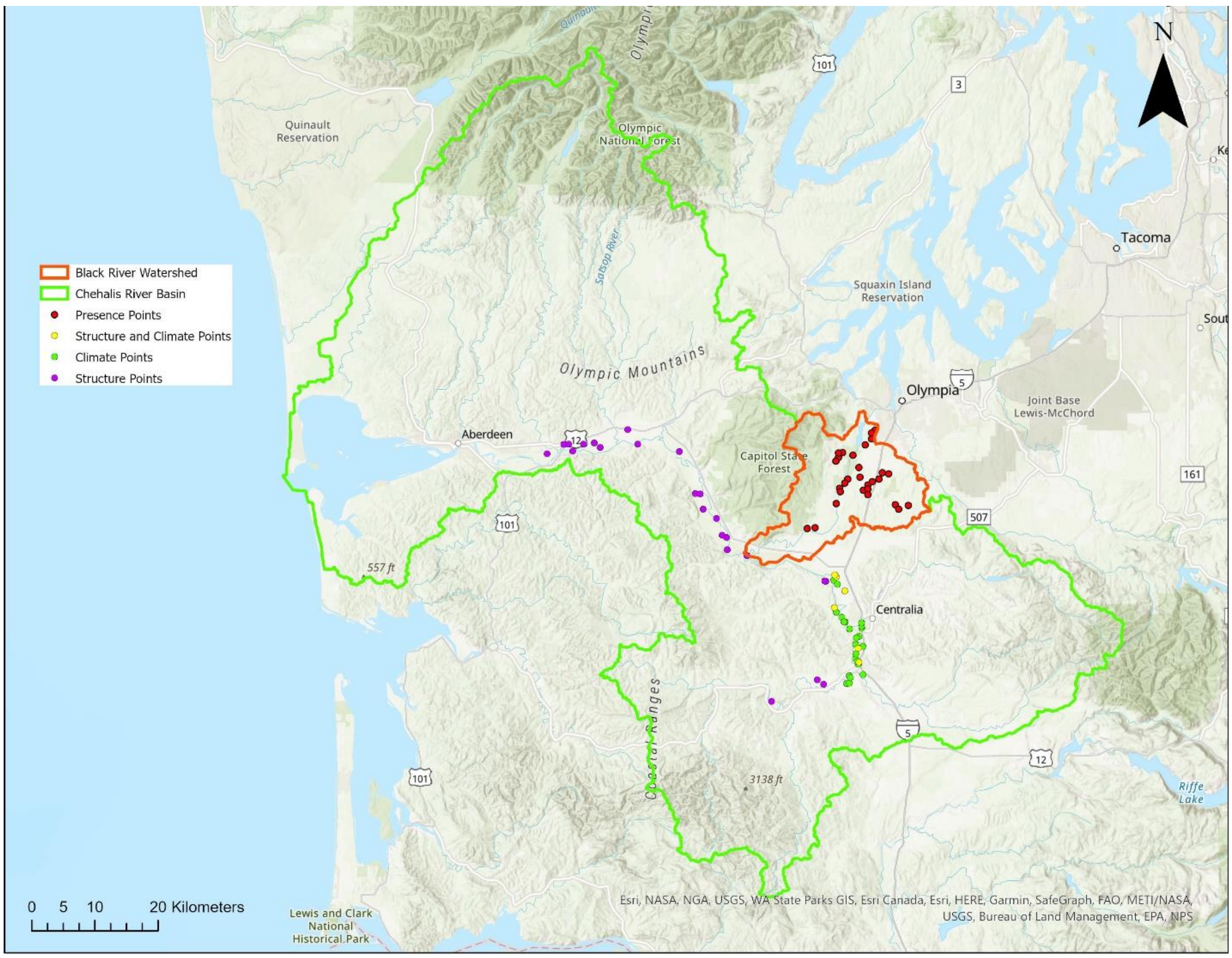
Threshold	Model	Success Rate	Omission Rate	p-value
MTP	Structure	0.965517	0.034483	0
	Climate	0.862069	0.137931	0.071904
10TP	Structure	0.896552	0.103448	0
	Climate	0.793103	0.206897	0.022506

Appendix 4. The percent contribution and permutation importance of the variables in the structure-only model.

Variable	Percent Contribution	Permutation Importance
Proximity to Cover Class	35.9	69.5
Landcover	29.1	8.7
Hydric Soil	28.4	5.8
Herbaceous Vegetation Height	4.4	2
Slope	2.2	14.1

Appendix 5. The percent contribution and permutation importance of the variables in the climate-only model.

Variable	Percent Contribution	Permutation Importance
Precipitation of Wettest Month	26.5	34.2
Mean Temperature of Coldest Quarter	24.4	14.9
Precipitation of Driest Quarter	24.4	17.6
Temperature Annual Range	15.6	18.4
Annual Mean Temperature	9	14.9



Appendix 6. Survey points selected according to the structure-only and climate-only Maxent outputs. Points were selected according to their probability of presence in the Maxent outputs (> 0.7).

Appendix 7. The comparison results of the environmental variables and abundance of exotic species between the Chehalis River floodplain survey points selected from the structure-only or climate-only models and the Black River presence points.

Comparison Results of Structure-only and Climate-only Variables

Variable	Structure Only Model Test	df	Statistic	p-value
Environmental Variables				
Distance to Habitat	Mann-Whitney U test		W= 420.5	1.0000
Herbaceous Vegetation Height	Mann-Whitney U test		W= 393.5	0.6509
Landcover	Chi-squared test	2	X^2= 2.4211	0.2980
Slope	Mann-Whitney U test		W= 444	0.7098
Hydric Soil	Chi-squared test	1	X^2= 0	1.0000
Exotic Species Abundance Variables				
Centrarchid Abundance	Mann-Whitney U test		W= 218.5	**0.0002**
Bullfrog Abundance	Mann-Whitney U test		W= 100.5	**0.0000**

Variable	Climate Only Model Test	df	Statistic	p-value
Environmental Variables				
Annual Mean Temperature	Welch Two Sample t-test	51.555	t= -8.6819	**0.0000**
Mean Temperature of Coldest Quarter	Mann-Whitney U test		W= 0	**0.0000**
Precipitation of Wettest Month	Mann-Whitney U test		W= 731	**0.0000**
Precipitation of Driest Quarter	Welch Two Sample t-test	49.754	t= -10.85	**0.0000**
Temperature Annual Range	Mann-Whitney U test		W= 681	**0.0000**
Exotic Species Abundance Variables				
Centrarchid Abundance	Mann-Whitney U test		W= 122.5	**0.0000**
Bullfrog Abundance	Mann-Whitney U test		W= 79.5	**0.0000**

Appendix 8. Summary statistics for the environmental variables used in the Maxent models and the abundance of exotic species for the presence points in the Black River and the survey points selected from the structure-only model and the climate-only model.

Summary Statistics of Structure-only and Climate-only Variables

	Black		Structure-Only	
Variable	Mean	St Dev	Mean	St Dev
Environmental Variables				
Distance to Habitat (Meters)	6.21	12.37	6.21	12.37
Herbaceous Vegetation Height (Height Rank)	1.24	1.12	1.41	1.43
Landcover	Categorical			
Slope (Degrees)	0.54	0.57	0.45	0.47
Hydric Soil	Categorical			
Exotic Species Abundance Variables				
Centrarchid Abundance (Abundance Rank)	0.10	0.31	0.86	0.88
Bullfrog Abundance (Abundance Rank)	0.45	0.51	1.55	0.63

	Black		Climate-Only	
Variable	Mean	St Dev	Mean	St Dev
Environmental Variables				
Annual Mean Temperature (°C)	10.31	0.09	10.56	0.12
Mean Temperature of Coldest Quarter (°C)	4.32	0.09	4.75	0.11
Precipitation of Wettest Month (Millimeters)	212.15	5.52	204.04	4.69
Precipitation of Driest Quarter (Millimeters)	96.07	2.26	101.61	1.56
Temperature Annual Range (°C)	24.69	0.40	24.27	0.26
Exotic Species Abundance Variables				
Centrarchid Abundance (Abundance Rank)	0.10	0.31	1.28	0.84
Bullfrog Abundance (Abundance Rank)	0.45	0.51	1.62	0.56

Appendix 9. Contingency tables for (a) landcover and (b) hydric soil, the categorical variables used in the structure-only model.

The Frequency of Points Occurring in Land Cover Class and Hydric Soils

(a)

Landcover Class Frequency

	Black	Chehalis
Non-habitat	6	6
Agriculture	6	2
Emergent Wetland	17	21

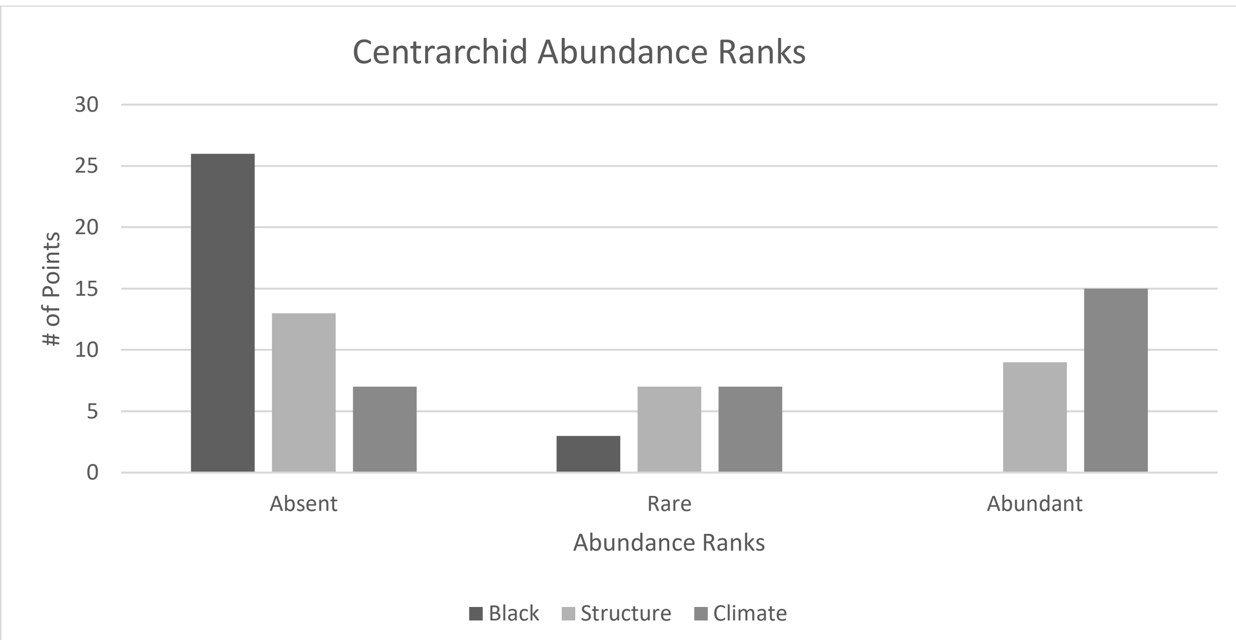
(b)

Hydric Soil Frequency

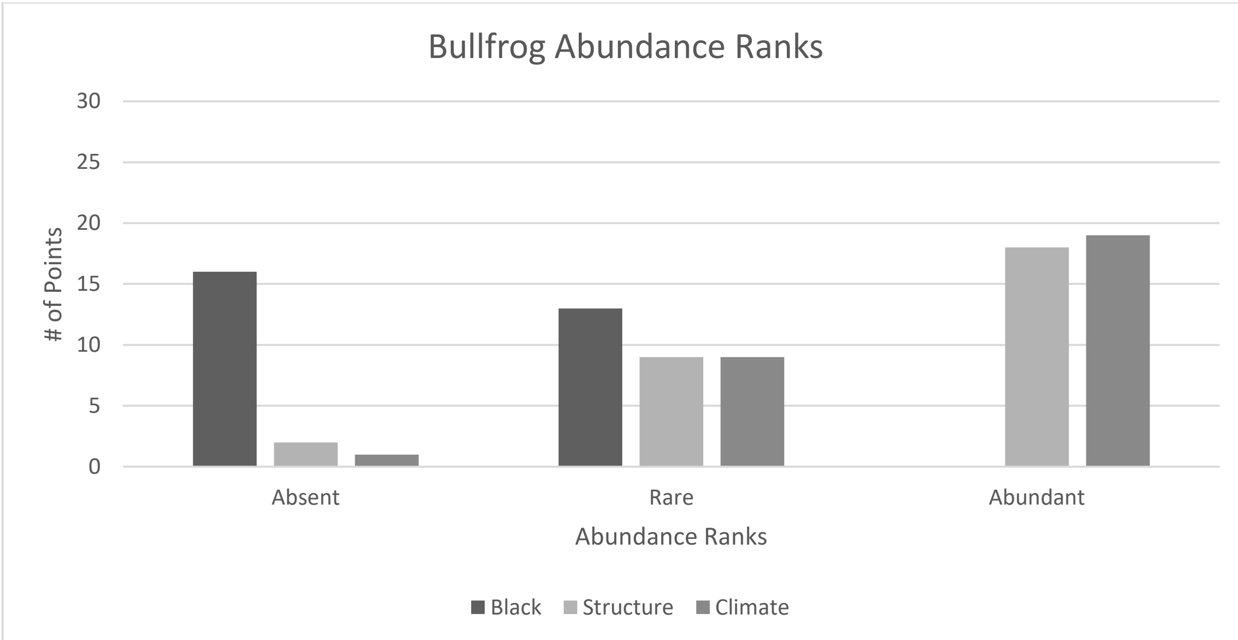
	Black	Chehalis
Non-Hydric	6	7
Hydric	23	22

Appendix 10. The magnitude of change between statistically different variables in the structure-only and climate-only models.

Magnitude of Change in Statistically Different Variables		
Variable	Difference	Direction
Climate-Only Variables		
Annual Mean Temperature (°C)	0.25 °C	C warmer than B
Mean Temperature of Coldest Quarter (°C)	0.43 °C	C warmer than B
Precipitation of Wettest Month (Millimeters)	8.11 mm	C drier than B
Precipitation of Driest Quarter (Millimeters)	5.54 mm	C wetter than B
Temperature Annual Range (°C)	0.41 °C	C narrower than B
Climate-only Exotic Species Abundance Variables		
Centrarchid Abundance (Abundance Rank)	1.17	C more abundant than B
Bullfrog Abundance (Abundance Rank)	1.17	C more abundant than B
Structure-only Exotic Species Abundance Variables		
Centrarchid Abundance (Abundance Rank)	0.76	C more abundant than B
Bullfrog Abundance (Abundance Rank)	1.10	C more abundant than B

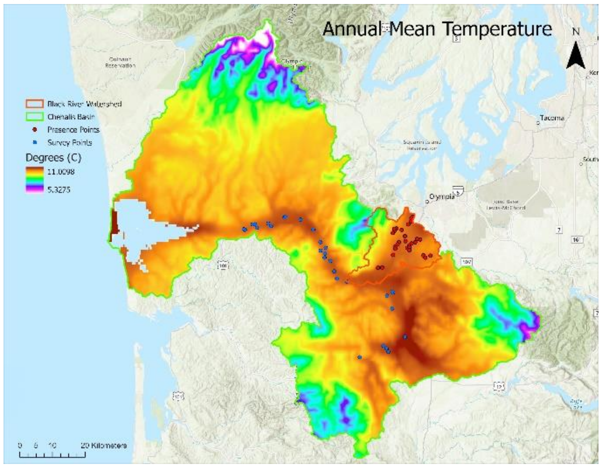


Appendix 11. The abundance ranks of centrarchid fishes at the Black River presence points and the Chehalis River floodplain survey points selected in the structure-only model and the climate-only model.

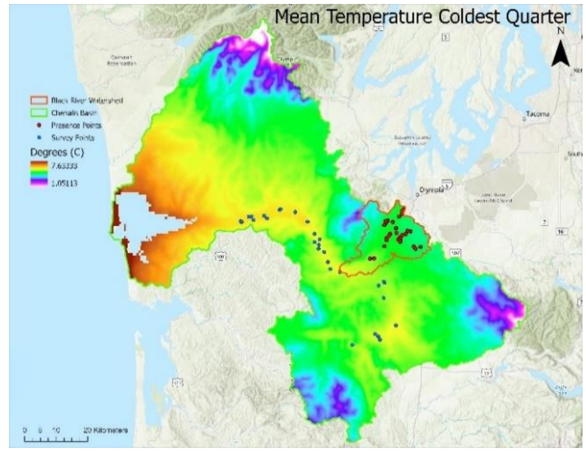


Appendix 12. The abundance ranks of bullfrogs at the Black River presence points and The Chehalis River floodplain survey points selected in the structure-only model and the climate-only model.

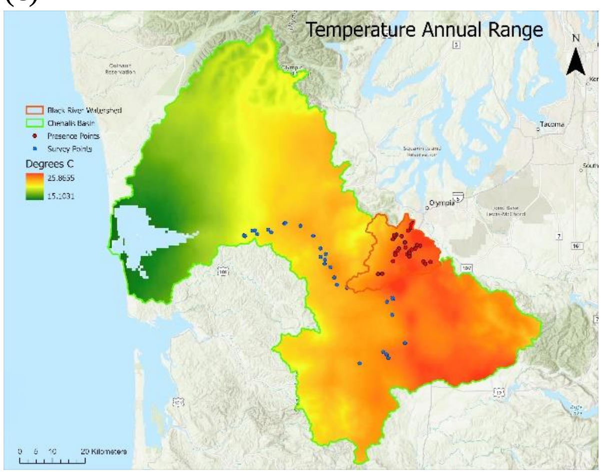
(a)



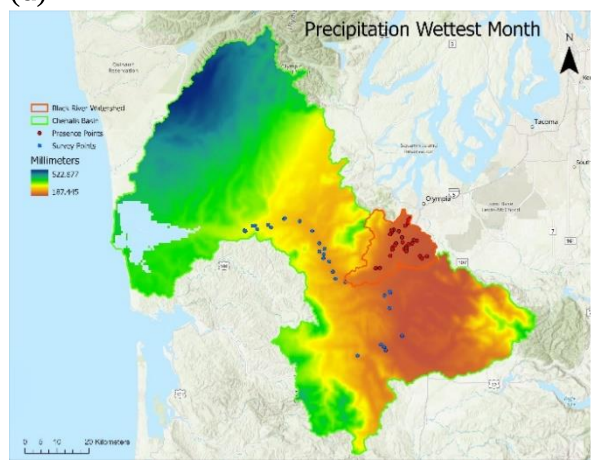
(b)



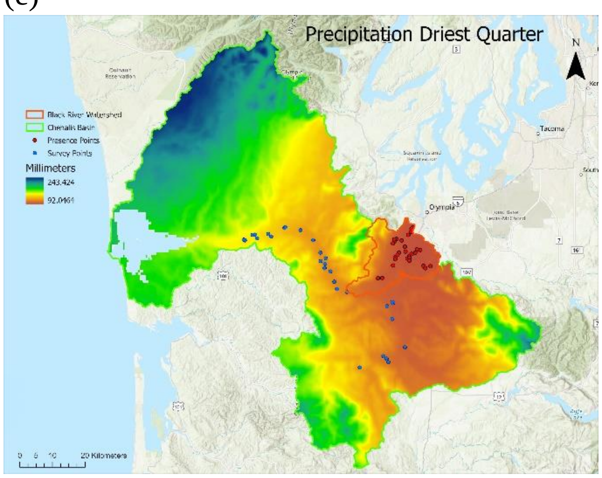
(c)



(d)



(e)



Appendix 13. Selected climate variables for the Maxent model.