

Winners and losers over a ½ century of change in crayfish assemblages of Wyoming, USA

Braxton M. Newkirk^{1,4}, Eric R. Larson^{2,5}, Andrew D. Walker^{1,6}, and Annika W. Walters^{3,7}

¹Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, 1000 East University Avenue, University of Wyoming, Laramie, Wyoming 82071 USA

²Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 1102 South Goodwin Avenue, Urbana, Illinois 61801 USA

³US Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology and Program in Ecology, 1000 East University Avenue, University of Wyoming, Laramie, Wyoming 82071 USA

Abstract: Crayfish have experienced extensive assemblage reorganization as a result of global change, with some species becoming globally invasive and others becoming rare or extinct. We combined historical and contemporary sampling data to determine temporal trends of crayfish assemblages of Wyoming, USA, identifying winners and losers over a ½ century of change (1969–2020). We first documented range expansions of several species, including the Virile Crayfish *Faxonius virilis* (Hagen, 1870), Ringed Crayfish *Faxonius neglectus* (Faxon, 1885), and Rusty Crayfish *Faxonius rusticus* (Girard, 1852) as well as range contractions of the Calico Crayfish *Faxonius immunis* (Hagen, 1870) and Pilose Crayfish *Pacifastacus gambelii* (Girard, 1852). We then used multispecies occupancy models to investigate potential mechanisms behind the replacement of *F. immunis* by *F. virilis* as the most commonly detected crayfish species in Wyoming over time. We hypothesized that *F. virilis* is more likely to competitively displace *F. immunis* from more permanent waterbodies, whereas *F. immunis* is more likely to persist in more ephemeral habitats because of its superior burrowing ability and tolerance of low dissolved oxygen concentrations. Our occupancy models supported this prediction, with *F. immunis* occupancy declining at more permanent sites in the presence of *F. virilis*, but *F. immunis* occupancy was unaffected by *F. virilis* in less permanent sites. We also found positive associations of *F. virilis* occupancy and detection probability with water temperature, suggesting that warmer streams may be more vulnerable to new invasions or spread by this species in nonnative regions of western North America. Our results highlight the value of regular, statewide crayfish surveys through documenting substantial changes in Wyoming's crayfish assemblage structure that may be driven by habitat-mediated competitive interactions.

Key words: competition, *Faxonius immunis*, *Faxonius neglectus*, *Faxonius rusticus*, *Faxonius virilis*, invasive species, *Lacunicambarus nebrascensis*, occupancy modeling, *Pacifastacus gambelii*

Freshwater ecosystems throughout the world are threatened by global change, which includes the introduction of nonnative invasive species, habitat fragmentation and degradation, and rapid anthropogenic climate change (Tickner et al. 2020). These complex, interacting global change factors are causing extensive reorganization of ecological communities (Jones et al. 2017, Dornelas et al. 2019). Community reorganization is not random; rather, sensitive species are lost while opportunistic or tolerant species increase in prevalence (Byrnes et al. 2007, Zavaleta et al. 2009, Moore and Olden 2017). As such, global change winners and losers are driving biotic homogenization (i.e., increased similarity be-

tween communities) for many taxa and regions (Olden et al. 2018).

Freshwater crayfishes are no exception to the phenomenon of global change winners and losers (Olden et al. 2011, Smith et al. 2019, Larson and Pool 2020). Some crayfishes have become globally invasive species through human introductions (Oficialdegui et al. 2020), whereas others have become more common by capitalizing on land-use changes that increase prevalence of their preferred habitat (Rhoden et al. 2016a). Other crayfishes have experienced population declines or extinctions (Light et al. 1995) due to displacement by invasive crayfishes (Perry et al. 2001, Martín-Torrijos

E-mail addresses: ⁴bnewkirk01@outlook.com; ⁵erlarson@illinois.edu; ⁶walkerandy1997@gmail.com; ⁷annika.walters@uwyo.edu

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et al. 2019) or habitat loss and degradation from land-use change (Welch and Eversole 2006, Welsh and Loughman 2015). Approximately a dozen crayfishes (<3% of total species) are globally invasive species (Lodge et al. 2012), whereas 191 crayfish species (32% of total species) are facing some risk of extinction (Richman et al. 2015). Although the effects of climate change on crayfish remain understudied (Westhoff and Rosenberger 2016, Krause et al. 2019), climate change is likely to exacerbate these patterns of winners and losers among freshwater crayfish assemblages (Capinha et al. 2013, Dunn et al. 2021).

Western North America has few native crayfishes relative to the species-rich southeastern USA, yet this depauperate region still faces considerable challenges in the management of both invasive and rare endemic crayfish species (Larson and Olden 2011, Pearl et al. 2013). For example, widespread invasive crayfishes in western North America have caused effects ranging from declines in native amphibian populations (Gamradt and Kats 1996) to potential increases in human disease risk (Bucciarelli et al. 2019). Alternatively, crayfishes endemic to western North America have experienced extinction (Bouchard 1977) and listings under the United States Endangered Species Act (USFWS 1988), with invasive crayfish species implicated in these population declines (Light et al. 1995, Egly and Larson 2018). In fact, nonnative crayfish species richness is now higher than native crayfish species richness for many regions of western North America (Larson and Olden 2011, Pearl et al. 2013, Larson and Pool 2020).

The state of Wyoming, USA, is an interesting location to study crayfish assemblages in western North America because it spans a continental divide that separates the native ranges of North America's 2 crayfish families: the species-poor Astacidae, which occur west of the Continental Divide, and the species-rich Cambaridae, which occur east of the Continental Divide (Lodge et al. 2012). Wyoming has the benefit of a ½ century of surveys for its crayfish assemblages, including a study on the crayfish of Yellowstone National Park initiated in 1969 (Dean et al. 1975), statewide crayfish inventories completed in the 1980s (Hubert 1988) and 2000s (Hubert 2010), and a recent conservation status assessment for the endemic species of the family Astacidae (Egly and Larson 2018). These crayfish surveys have occasionally failed to detect Wyoming's less common native crayfish species (Hubert 2010) while also discovering biological invasions like those by the Rusty Crayfish *Faxonius rusticus* (Girard, 1852) (WGFD 2010). In addition, in recent decades, surveys have documented a shift from Calico Crayfish *Faxonius immunis* (Hagen, 1870) to Virile Crayfish *Faxonius virilis* (Hagen, 1870) as Wyoming's most prevalent species (Hubert 2010).

In this study, we sought to understand patterns and potential drivers of Wyoming's native and invasive crayfish species prevalence through time. To do this, we resampled

Wyoming's crayfish assemblages, including surveying for invasive crayfishes, and used historical sources to identify and characterize temporal distributional patterns, similar to recent studies for other states and regions (Olden et al. 2006, Peters et al. 2014, Smith et al. 2019). Beyond identifying winners and losers through time, we used multispecies occupancy models (Rota et al. 2016) based on contemporary data to identify potential drivers for *F. virilis* becoming more common while *F. immunis* declined. We chose to do this because Bovbjerg (1970) found that *F. virilis* was competitively dominant over *F. immunis* in permanent streams or waterbodies of Iowa, USA, but that *F. immunis* persisted in intermittent or ephemeral habitats because of its superior burrowing ability and tolerance of low dissolved oxygen concentrations. We hypothesized that *F. virilis* replacement of *F. immunis* over time in Wyoming might be similarly mediated by habitat, as has been observed for other crayfish species replacements (Olden et al. 2011, Smith et al. 2019). Altogether, we characterized changes in Wyoming's crayfish assemblages and investigated mechanisms underlying shifts in prevalence of common species over a ½ century.

METHODS

We compiled data from multiple historical sources in combination with field surveys at 289 contemporary crayfish sites in Wyoming to examine the prevalence of each of Wyoming's crayfish species and to identify temporal trends in crayfish assemblages. In addition, we used multispecies occupancy models with field data from 125 sites to assess potential drivers of the shift in prevalence exhibited by *F. virilis* and *F. immunis*.

Study region and species

Watersheds of Wyoming drain the Rocky Mountains and high plains of the western USA, spanning a continental divide between Atlantic-draining Missouri and Platte river tributaries and Pacific-draining Snake and Colorado river tributaries (Fig. 1). This continental divide encloses an endorheic basin, the Great Divide Basin, which does not drain to an ocean. Similarly, the Bear River of far southwestern Wyoming drains to the Great Salt Lake of the Bonneville Basin without an ocean terminus but shares some freshwater species, like the Pilose Crayfish *Pacifastacus gambelii* (Girard, 1852), with the adjacent, Pacific-draining Snake River.

Crayfish assemblages of Wyoming have been inventoried by occasional statewide surveys (Hubert 1988, 2010), often using opportunistic collections by the Wyoming Game and Fish Department (WGFD) as well as more narrow studies focusing on locations like Yellowstone National Park (Dean et al. 1975), individual native species (Egly and Larson 2018), or newly discovered populations of invasive *F. rusticus* (WGFD 2010, 2021). These studies identified 5 crayfish species as native somewhere within Wyoming and 1 species,

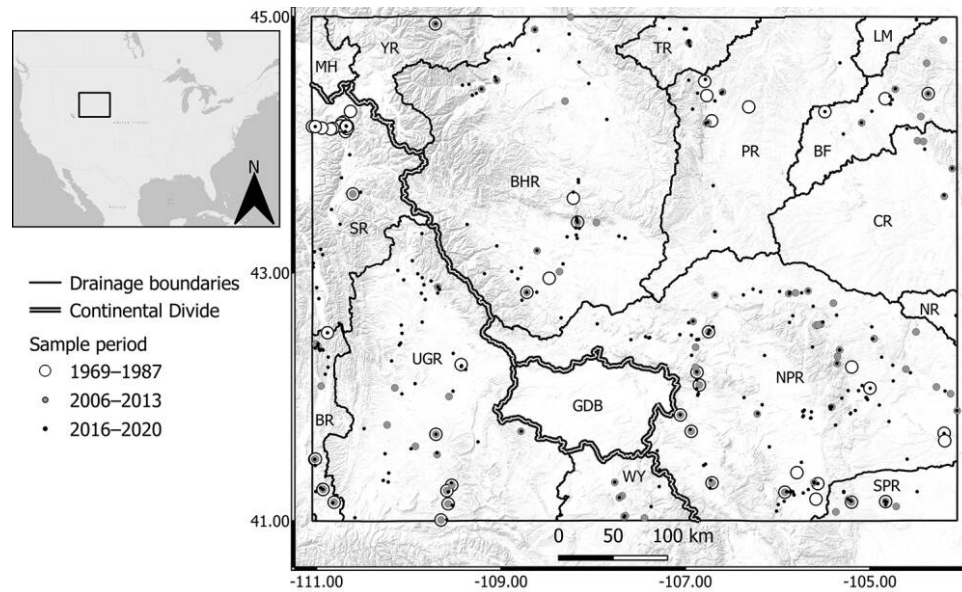


Figure 1. Wyoming, USA (inset), with latitude and longitude (WGS84) axes and sites of crayfish sampling by time periods (1969–1987, 2006–2013, 2016–2020) across watershed boundaries (Hydrologic Unit Code 6; NHDPlus V2). The Continental Divide between Atlantic (east) and Pacific (west) draining rivers is white with double black lines, enclosing the Great Divide Basin (GDB). Drainage code identifiers: BF = Belle Fourche River, BHR = Big Horn River, BR = Bear River, CR = Cheyenne River, LM = Little Missouri River, MH = Missouri Headwaters, NPR = North Platte River, NR = Niobrara River, PR = Powder River, SPR = South Platte River, SR = Snake River, TR = Tongue River, UGR = Upper Green River, WY = White-Yampa River, YR = Yellowstone River.

F. rusticus, as entirely nonnative to the state. Both *F. immunis* and *F. virilis* are native east of the Continental Divide in Wyoming, but both have established nonnative populations in the historically crayfish-free upper Colorado River drainages (Hubert 1988, 2010). Further, *F. virilis* has become widespread in the Bear River drainage, where it may be competitively displacing the native *P. gambelii* as an invasive species (Hubert 2010, Egly and Larson 2018). Among nonnative or invasive crayfishes within Wyoming, *F. rusticus* was recently discovered in 2006 at localized sites in the North Platte River drainage and has been the focus of eradication and control efforts (WGFD 2010, 2021).

Several native crayfish species have historically been known from highly localized or limited distributions within Wyoming. The Ringed Crayfish *Faxonius neglectus* (Faxon, 1885) was only occasionally detected in the vicinity of several reservoirs in the upstream South Platte River drainage of far southeastern Wyoming (Hubert 1988, 2010). Similarly, the Great Plains Mudbug *Lacunicambarus nebrascensis* (Girard, 1852), recently revised from *Cambarus diogenes* Girard, 1852 by Glon et al. (2022), was known from only a single tributary of the North Platte River in southeastern Wyoming (Hubert 1988). *Lacunicambarus nebrascensis* is notable for being Wyoming's only primary burrowing, or semiterrestrial, crayfish. Last, *P. gambelii* occurred historically in both the Bear and Snake river drainages of western Wyoming (Dean et al. 1975, Hubert 1988, 2010) but has been replaced at many Bear River sites by *F. virilis* (Egly and Larson 2018). At the on-

set of our study, *F. neglectus*, *L. nebrascensis*, and *P. gambelii* were each perceived as at risk of loss or extirpation from Wyoming because of their limited range extents.

Contemporary crayfish collections

Between 28 April 2020 and 4 November 2020, we surveyed Wyoming crayfish assemblages at 289 sites consisting of 161 lotic sites and 128 lentic sites. Crayfish collections were made by our authorship team and colleagues at WGFD. We selected sample sites nonrandomly to revisit historical sampling sites and because of constraints of land ownership and access. We prioritized historical sites and new sites within drainages with low historical sampling coverage by past statewide surveys (Hubert 1988, 2010). If historical sampling sites were inaccessible because of changes in land ownership, we chose nearby publicly accessible sites. Some regions with scarce surface water, like the Great Divide Basin, were not sampled (Fig. 1). We collected crayfish using active searches and passive baited traps, although some WGFD collections consisted of incidental crayfish capture during fish sampling using other methods (e.g., backpack electrofishing, gill netting; see Table 1 for no. of sites for each sampling method). For both active and passive collection methods, we targeted areas with structure such as rocks, macrophytes, or woody debris because crayfish often use these areas as shelter (Magoulick et al. 2017, Smith et al. 2019). At every site we sampled, we used a YSI probe (model Pro 2030; Yellow

Table 1. Data sources for analyses of crayfish assemblage change by time in Wyoming, USA, grouped by time period and with y sampled, whether the data recorded were presence/absence or presence only, and gear used for crayfish collection. Effort (no. of sites) by gear type is given for our 2020 sampling only.

Time period	Source	Sample year	Type of data	Gear (effort)
1969–1987	Dean et al. 1975	1969–1971 and 1974	Presence/absence	Active by hand or net
	Hubert 1988	1985–1987	Presence	Opportunistic during fish sampling
2006–2013	Hubert 2010	2007–2009	Presence	Traps, seines, dip nets, gill nets, trammel nets
	WGFD 2010	2006–2007	Presence	Traps
	WGFD 2021	2012–2013	Presence	Unknown
2016–2020	Egly and Larson 2018	2016	Presence/absence	Baited traps, active searches
	This study	2020	Presence/absence	Active (164), baited traps (95), electrofishing (18), unknown (10), gill net (8), fyke nets (4)

Springs Instruments, Yellow Springs, Ohio) to measure water temperature at the time of sampling (°C). Also at every site, we tried to voucher ≥ 1 male crayfish of each species for later identification. Crayfish collected by WGFD colleagues were transferred to the authorship team for species identification and vouchering at the University of Wyoming in Laramie, Wyoming. We identified crayfish following Taylor et al. (2015) and Principe et al. (2021).

For active searches we used a combination of dip nets and kick seines (~1 m long, 6.3 mm mesh) and sampled in teams of 2 to 4 people. During active searches, we attempted to sample 100 to 200 m of stream or shore length, moving from downstream to upstream at lotic sites. We performed three 20-min timed searches at each site (separated in space) to provide replicated observations for estimating crayfish detection probabilities (see below). These 3 replicated timed searches were conducted together by the entire sampling crew. After each 20-min timed search, we released the captured crayfish and moved to a new area within the study site to prevent recaptures and to sample other habitat types. Occasionally, weather or logistical constraints limited us to fewer than three 20-min timed searches at a site (7 sites with 1 replicate, 9 sites with 2 replicates).

At sites that we were unable to effectively sample using active searches, we used passive sampling by baited traps. We also opportunistically passively sampled some sites with baited traps for convenience (i.e., trapping overnight at sites near crew lodging). Baited traps were cylindrical, wire-mesh Gee's minnow traps (length of 46 cm and diameter of 23 cm at the widest point) with 2 enlarged openings of 4 to 6 cm, consistent with those used for crayfish surveys in North America (Larson and Olden 2016). We set a total of 6 traps, each baited with 240 mL of dry dog food, at each site across ~100 m of stream length or shoreline. We set traps at 1 to 2 m depth in areas with slower moving current (lotic sites) or protected from large wave exposure (lentic sites). We set traps in the afternoon and retrieved them the following morning.

Trends of assemblage change

We combined historical and contemporary data to characterize crayfish assemblage change over a ½ century for Wyoming (1969–2020). We assigned historical and contemporary data into 3 time periods (Table 1): 1969 to 1987 (Dean et al. 1975, Hubert 1988), 2006 to 2013 (Hubert 2010, WGFD 2010, 2021), and 2016 to 2020 (Egly and Larson 2018, this study). We created these 3 time periods to include 1 statewide survey in each (Hubert 1988, 2010, our contemporary survey), combining these statewide surveys with other sources of Wyoming crayfish data collected closest in time. Previous sources of Wyoming crayfish data used a variety of sampling methods that are detailed in Table 1.

Some historical data sources recorded only crayfish presence data and not absences at sites where no crayfish were detected (Table 1). Accordingly, we analyzed crayfish assemblage change through time as the proportion of sites occupied by each species relative to the total number of sites where crayfish were found, omitting absence records. This approach follows past analyses for crayfish assemblage change where absence data were not available, with this lack of absence data often being due to using element occurrences from museum or similar sources (Olden et al. 2006, Peters et al. 2014). We also omitted 14 sites where crayfish were identified only to genus (*Faxonius*) and not species from Hubert (2010). Including this omission, crayfish sampling effort and detections increased over time, from 47/57 sites (82%) with crayfish detected for 1969 to 1987, to 78/78 sites (100%) with crayfish detected for 2006 to 2013, to 189/297 sites (64%) with crayfish detected for 2016 to 2020. We updated any sites resampled within the same time period to the most recent presence/absence data (i.e., Egly and Larson 2018 were updated to our 2020 survey).

Multispecies occupancy models

We investigated potential mechanisms for replacement of *F. immunis* as Wyoming's most commonly detected crayfish

species by *F. virilis* between Hubert (1988) and Hubert (2010) using multispecies occupancy models (Rota et al. 2016). These models allowed us to infer occupancy of 1 species (*F. immunis*) contingent on occupancy of the other (*F. virilis*) while simultaneously accounting for habitat effects on occupancy and imperfect detection of each species individually (MacKenzie et al. 2002). We built occupancy models using data from the 125 active search sites sampled by our authorship team, where the replicated 20-min searches separated in space were the units for estimating detection probability. We omitted other sample types from 2020 (e.g., collected by WGFD) because they reported sampling effort less consistently than the searches by our team.

We used published literature for *F. immunis* and *F. virilis* and similar crayfish species to identify environmental predictors for modeling both occupancy and detection probability (Table 2). For occupancy estimation, we used several predictor variables from the United States Environmental Protection Agency's StreamCat database (<https://www.epa.gov/national-aquatic-resource-surveys/streamcat-dataset>; Hill et al. 2016), including baseflow index, index of catchment integrity, and mean summer water temperatures. Baseflow index refers to the contribution of overall stream flow from groundwater inputs (%), where higher baseflow index values are associated with more permanent waters (Hill et al. 2016). Because this metric was derived for lotic sites, we modified the baseflow index values at our lentic sites to the

maximum value (100%), with the assumption that our lentic sites remain wetted throughout the year. We anticipated that *F. immunis* would be more tolerant of low baseflow index values than *F. virilis* given its superior burrowing ability and tolerance of low dissolved oxygen concentrations but that *F. immunis* occupancy would decline at more permanent sites because of competitive displacement by *F. virilis* (Bovbjerg 1970). We included index of catchment integrity, which is a modeled prediction of stream reach condition at a catchment scale derived using a variety of other stream health indices (Hill et al. 2016), because *F. virilis* has been associated with degraded habitats in its nonnative range (Light et al. 1995). We included mean summer water temperatures, modeled using water temperature data from United States Geological Survey temperature sites (Hill et al. 2013), because both *F. immunis* and *F. virilis* are warmwater species that may perform poorly in cooler or higher elevation study sites (Wetzel and Brown 1993, Westhoff and Rosenberger 2016). We applied lotic temperature estimates to lentic sites. We also included several predictor variables from the National Hydrography Dataset (NHDPlus V2; <https://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus>) including stream slope (m/m) and mean annual discharge (m³/s). We used mean annual discharge as an indicator of waterbody size because crayfish species can differ in their habitat preferences for smaller or larger habitats (Nolen et al. 2014). Like mean summer water temperature, discharge

Table 2. Covariates for modeling Wyoming, USA, crayfish occupancy and detection probabilities of *Faxonius immunis* and *Faxonius virilis*, units of measure, data sources, and predictions.

Covariate	Variable	Unit	Data source	Prediction
Occupancy	Baseflow index	%	StreamCat baseflow index values derived for each catchment (Hill et al. 2016)	<i>F. immunis</i> occupancy will decrease and <i>F. virilis</i> occupancy will increase with increased baseflow index values.
	Index of catchment integrity	Proportion	StreamCat index of catchment integrity values derived using multiple environmental variables (Hill et al. 2016)	<i>F. virilis</i> occupancy will increase with decreased index of catchment integrity values.
	Mean summer water temperature 2014	°C	StreamCat mean summer water temperatures from 2014 (Hill et al. 2016)	<i>F. immunis</i> and <i>F. virilis</i> occupancy will increase with increased mean summer water temperatures.
	Mean annual discharge	m ³ /s	NHDPlusV2 EROM estimates from 1971–2000	Crayfish occupancy can be affected by habitat size.
	Stream slope	m/m	NHDPlusV2 slope based on smoothed elevations	<i>F. immunis</i> and <i>F. virilis</i> occupancy will decrease with increased stream slope.
Detection	Mean annual discharge	m ³ /s	NHDPlusV2 EROM estimates from 1971–2000	<i>F. immunis</i> and <i>F. virilis</i> detection probabilities will decrease in larger habitats.
	Stream slope	m/m	NHDPlusV2 slope based on smoothed elevations	<i>F. immunis</i> and <i>F. virilis</i> detection probabilities will decrease with increased stream slope.
	Water temperature at time of sampling	°C	Temperatures taken prior to sampling	<i>F. immunis</i> and <i>F. virilis</i> detection probabilities will increase with increased water temperature.

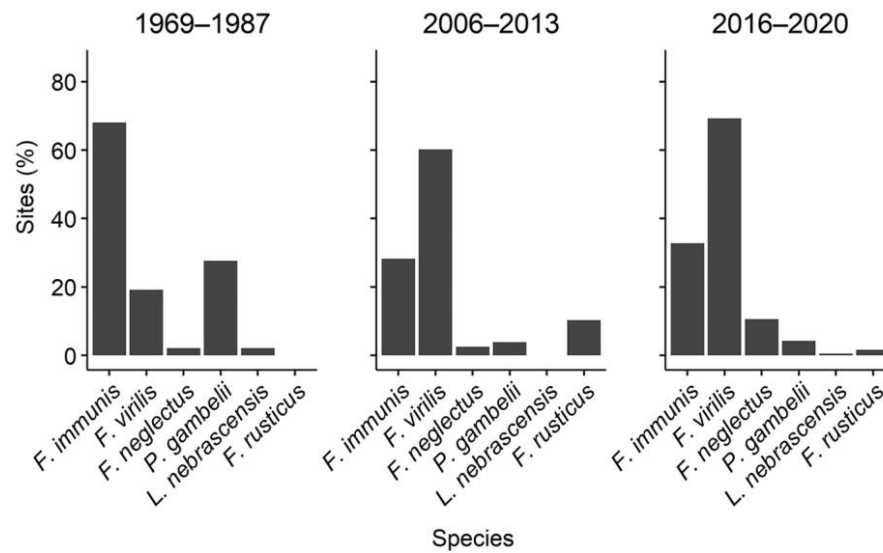


Figure 2. Prevalence of *Faxonius immunis*, *Faxonius virilis*, *Faxonius neglectus*, *Lacunicambarus nebrascensis*, *Pacifastacus gambelii*, and *Faxonius rusticus* in Wyoming, USA, by time period (see Table 1) as the % of sites at which each species was detected relative to all sites where crayfish were detected.

was used for both lotic and lentic sites. We included stream slope as an occupancy predictor because streams with high power (e.g., slope) can dislodge crayfish at high flows and reduce occupancy rates (Light 2003). Stream slope was derived for lotic sites, so we used the lowest value (0) for lentic sites.

We used both mean annual discharge and stream slope as well as the field measurement of water temperature at the time of sampling to model detection probabilities of the study crayfishes. We expected that higher mean annual discharge, corresponding with larger habitat area, could result in lower crayfish detection probability because larger habitats may be more difficult to comprehensively search (Larson and Olden 2016). We also suspected that streams with steeper slopes may have lower crayfish detection probabilities because active searches may be more difficult against higher current velocities (Magoulick et al. 2017). Last, we used water temperature at the time of sampling because crayfish activity levels increase with temperature, presumably increasing detection probabilities during warmer conditions (Johnson et al. 2014).

To build occupancy models, we used the package *unmarked* (version 1.0.1, Fiske and Chandler 2011) in the R program (version 4.0.4; R Project for Statistical Computing, Vienna, Austria). We first built single-species occupancy models (MacKenzie et al. 2002) for both *F. immunis* and *F. virilis* with all combinations of the above environmental variables to define subsequent candidate models for the multi-species occupancy models (Rota et al. 2016). We used well-supported single-species models (Δ Akaike Information Criterion corrected for small sample size [AICc] ≤ 2 as per Burnham and Anderson 2004) for both *F. immunis* and *F. vi-*

rilis as candidate models for multispecies occupancy estimation. Next, we built multispecies occupancy models with all combinations of the candidate models for *F. immunis* and *F. virilis*. Our multispecies models included models with no species interaction, constant species interaction, and species interaction mediated by baseflow index (our metric for stream permanence). Similar to our single-species models, we ranked the multispecies models using AICc, with well-supported models having a Δ AICc ≤ 2 (Burnham and Anderson 2004). For brevity and because of consistency between our well-supported models, we used our top-ranked (best-supported) model to predict occupancy and detection probabilities for well-supported covariates.

RESULTS

Trends of assemblage change

Crayfish species prevalence changed through time, with some species becoming more common and others more rare (Fig. 2). During the 1969 to 1987 time period, *F. immunis* was the most frequently detected species, but its prevalence decreased by the 2006 to 2013 and 2016 to 2020 time periods. In contrast, *F. virilis* increased in prevalence relative to 1969 through 1987 and was the most commonly detected crayfish in Wyoming in both 2006 to 2013 and 2016 to 2020. Similarly, *F. neglectus* increased in prevalence in 2016 to 2020, and *F. rusticus* increased in prevalence in 2006 to 2013, whereas *P. gambelii* experienced declines in prevalence by 2006 to 2013 that persisted from 2016 to 2020 (Fig. 2).

Along with changes in overall prevalence over time, there were also shifts in crayfish distributions within Wyoming from early to late time periods. The most apparent distributional

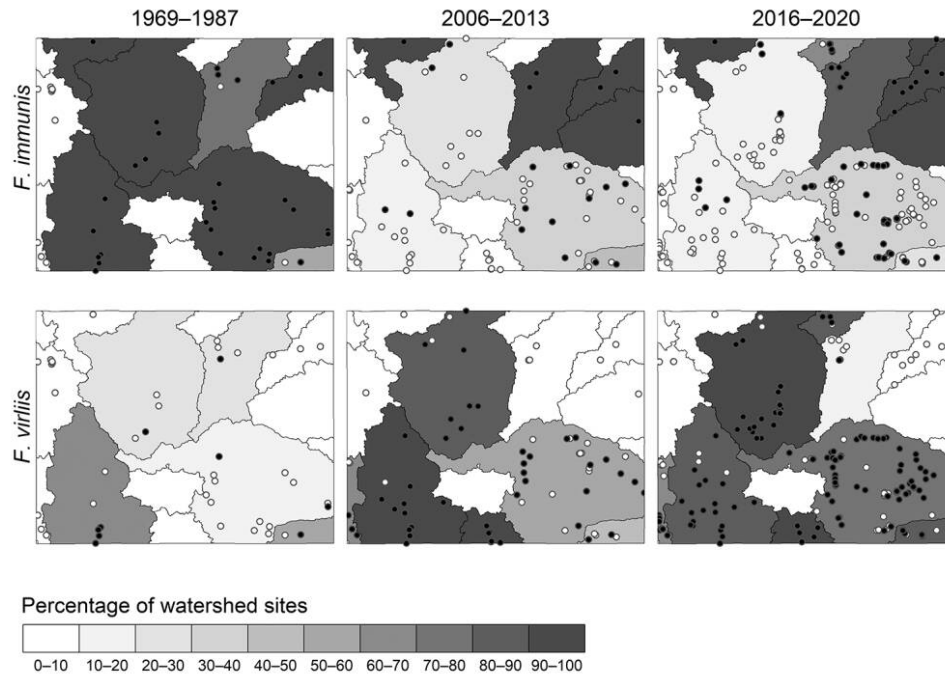


Figure 3. *Faxonius immunis* (top row) and *Faxonius virilis* (bottom row) presence (black points) and prevalence (shading as presences against nondetections, white circles) by time period (see Table 1) for major watersheds of Wyoming, USA. Nondetections are only from sites where other crayfish species were detected during the sampling period because some sources did not report absence data.

shifts occurred between *F. virilis* and *F. immunis* from 1969 through 1987 and 2006 through 2013, with *F. virilis* distributions expanding throughout much of Wyoming but *F. immunis* remaining the dominant species only in northeast Wyoming (Fig. 3). Other species also exhibited notable distributional changes over time. For example, *F. neglectus* expanded its distribution considerably into the North Platte and Niobrara River drainages in 2016 to 2020 (Fig. 4). Similarly, we detected distributional expansions of *F. rusticus* into the North Platte River drainage from 2016 through 2020 that were disjunct from previously discovered populations from 2006 to 2013. In contrast, *P. gambelii* experienced distributional declines in the Bear River of southwestern Wyoming from 2006 through 2013 and 2016 through 2020 relative to 1969 through 1987. Last, we confirmed *L. nebrascensis* presence in southeastern Wyoming from 2016 to 2020 despite its lack of detections from 2006 to 2013 (Fig. 4).

Multispecies occupancy models

Twenty multispecies occupancy models were well supported among all candidate models considered (i.e., $\Delta\text{AICc} < 2$; Table S1). Single-species models are not reported for brevity but recovered similar relationships for *F. immunis* and *F. virilis* occupancy and detection probability as our multispecies occupancy models (Tables S1–S3). Our best-supported model (Table 3) had a pseudo- R^2 of 0.33 and included mean annual discharge and mean summer water

temperature as occupancy covariates for *F. immunis*, mean summer water temperature and stream slope as occupancy covariates for *F. virilis*, water temperature at time of sampling as a detection covariate for *F. virilis*, and an effect of co-occurrence between these 2 species on occupancy contingent on baseflow index (Table 3). We interpret here our best-supported model as representative because all well-supported models included this hypothesized multispecies occupancy effect with baseflow, whereas no models that omitted co-occurrence effects between *F. virilis* and *F. immunis* and baseflow were well supported (i.e., $\Delta\text{AICc} > 2$; Table S1).

Faxonius immunis occupancy increased with warmer mean summer water temperatures and decreased with higher mean annual stream discharge (Fig. 5A, C). Accordingly, *F. immunis* occupancy was more likely in warmer but smaller habitats. Our index of catchment integrity was included as an occupancy covariate and discharge was included as a detection probability covariate for *F. immunis* in some well-supported models (Table S1), but both predictors had weak effects with high p -values and are not interpreted here. No other occupancy or detection probability predictors were included in well-supported multispecies models for *F. immunis*. *Faxonius virilis* occupancy also increased with warmer mean summer water temperatures (Fig. 5B), and *F. virilis* detection probability was strongly affected by water temperature at the time of sampling, with detection probability increasing sharply $>15^\circ\text{C}$ (Fig. 5D).

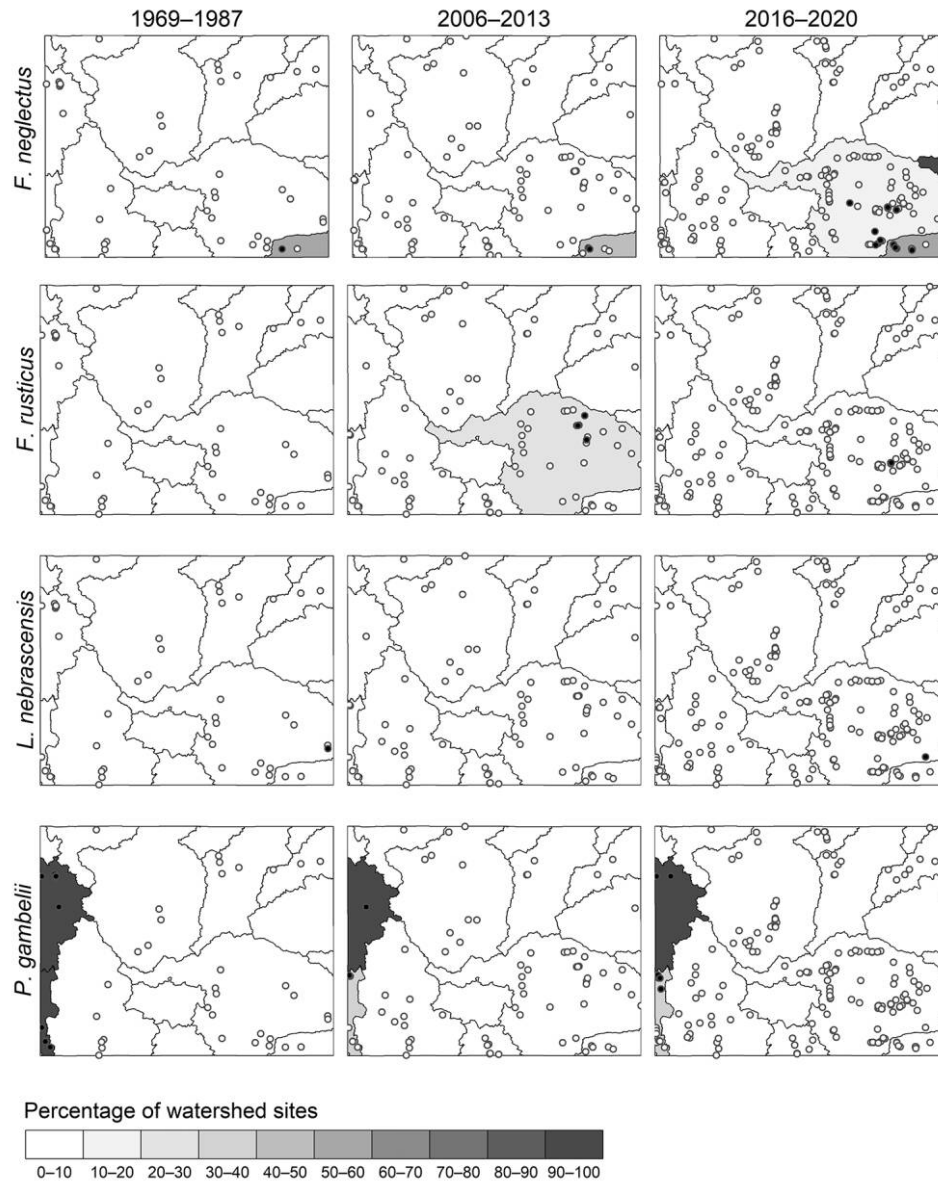


Figure 4. *Faxonius neglectus* (1st row), *Faxonius rusticus* (2nd row), *Lacunicambarus nebrascensis* (3rd row), and *Pacifastacus gambelii* (bottom row) presence (black points) and prevalence (shading as presences against nondetections, white circles) by time period (see Table 1) for major watersheds of Wyoming, USA. Nondetections are only from sites where other crayfish species were detected during the sampling period because some sources did not report absence data.

We do not interpret the effect of stream slope on either occupancy or detection probability for *F. virilis* because of weak effects and high p -values (Tables 3, S1). No other occupancy or detection probability predictors were included in well-supported multispecies models for *F. virilis*.

Our multispecies occupancy models supported our hypothesized effect of *F. virilis* on *F. immunis* occupancy mediated by stream permanence, represented by baseflow index (Table 3). *Faxonius immunis* occupancy exhibited a negative relationship with baseflow index, with this species less likely to occur in more permanent habitats. This relationship was

stronger when *F. virilis* was present at sites (Fig. 6). *Faxonius immunis* was especially unlikely to occupy sites with high baseflow index values when *F. virilis* was present, but the presence of *F. virilis* did not affect *F. immunis* occupancy at sites with low baseflow values.

DISCUSSION

Our study resampled Wyoming's crayfish assemblages to update knowledge regarding the distribution and prevalence of crayfish species in this state and to identify potential drivers

Table 3. Results from our best-supported multispecies occupancy model (see Table S3 for formulas and additional parameters) for *Faxonius immunis* and *Faxonius virilis* including single and multispecies coefficient estimates on the logit scale, SE, z -scores, and p -values. The z -score is the estimate divided by SE to standardize to a normal distribution for statistical tests.

Model type	Species	Covariate	Estimate	SE	z	$p(z)$
Occupancy	<i>F. immunis</i>	(Intercept)	-0.87	0.36	-2.44	0.02
		Mean annual discharge	-0.83	0.38	-2.18	0.03
		Mean summer water temperature	0.73	0.30	2.43	0.02
	<i>F. virilis</i>	(Intercept)	0.26	0.41	0.62	0.54
		Mean summer water temperature	0.55	0.31	1.78	0.08
Co-occurrence		Stream slope	-2.58	1.93	-1.34	0.18
		(Intercept)	-1.64	0.73	-2.25	0.03
Detection		Baseflow index	-1.15	0.60	-1.90	0.06
	<i>F. immunis</i>	(Intercept)	2.11	0.38	5.58	<0.001
	<i>F. virilis</i>	(Intercept)	0.88	0.32	2.72	0.01
		Water temperature at time of sampling	2.89	0.47	6.12	<0.001

of changing prevalence between 2 common species. We documented temporal and spatial changes in Wyoming crayfish assemblages over multiple decades, with some species becoming more common and others becoming more rare. For example, *F. immunis* and *P. gambelii* experienced pronounced distributional declines over time, whereas *F. neglectus*, *F. rusticus*, and especially *F. virilis* became more commonly detected. Our multispecies occupancy models support the hypothesis that a change in the most dominant

crayfish species from *F. immunis* to *F. virilis* is related to superior competitive performance of *F. virilis* in more permanent habitats, consistent with past work on these 2 species (Bovbjerg 1970). Future work might investigate potential effects of nonnative populations of *F. virilis* in Wyoming and western North America as well as potential effects of expanding populations of *F. neglectus* and *F. rusticus* that may influence native species, assemblages, and ecosystem processes (Twardochleb et al. 2013).

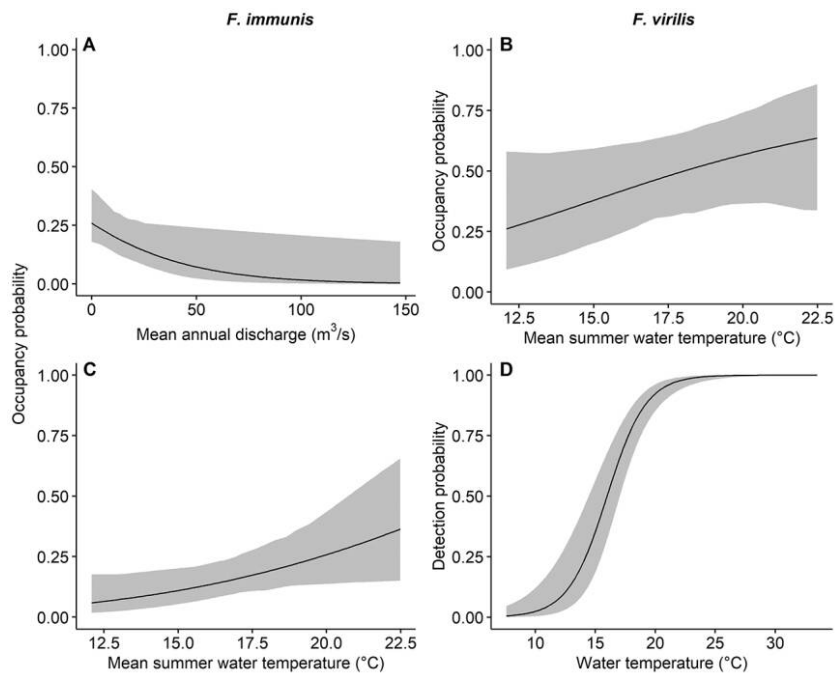


Figure 5. Estimated effects (solid lines) and 95% CI (gray ribbons) of mean annual discharge (A) and mean summer water temperature (C) on *Faxonius immunis* occupancy and estimated effects of mean summer water temperature on occupancy (B) and water temperature at time of sampling on detection probability (D) for *Faxonius virilis* from our best-supported model (see Table 3).

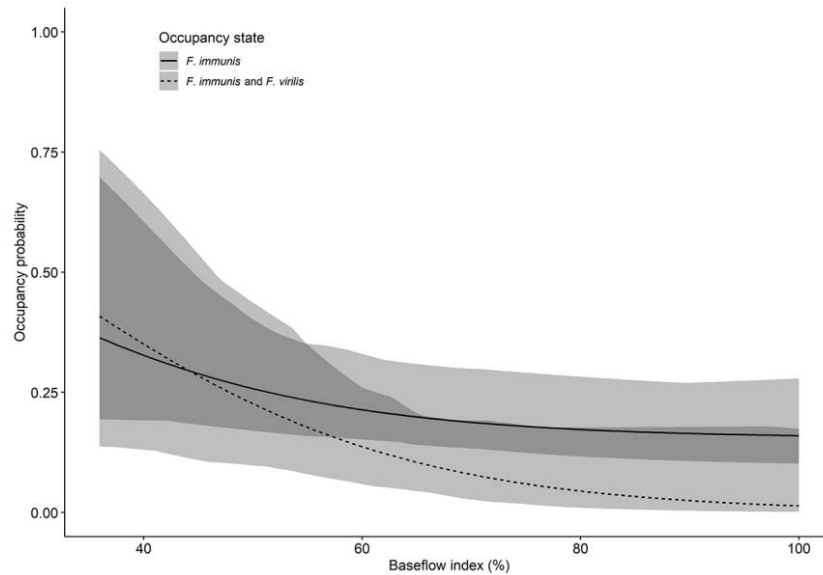


Figure 6. Estimated effects and 95% CI (gray ribbons) of baseflow index on *Faxonius immunis* occupancy in the presence (dashed) and absence (solid) of *Faxonius virilis* derived from our best-supported model (see Table 3).

Trends of assemblage change

Our study updated information on the status and distribution of Wyoming's 2 rarest native crayfish species, *L. nebrascensis* and *P. gambelii*. We confirmed the presence of *L. nebrascensis* in a watershed in far southeastern Wyoming where it had not been documented since Hubert's 1988 survey. This primary burrowing crayfish has received increased taxonomic and ecological scrutiny in recent years (Glon et al. 2022), and future work on its ecology and population trends within Wyoming would be useful for its management. Our findings also supported those of Hubert (2010) and Egly and Larson (2018) that *P. gambelii* has experienced pronounced population and distributional declines, particularly in the Bear River drainage of southwestern Wyoming, where this species has been widely replaced by non-native *F. virilis* populations. Mechanisms of possible effects of *F. virilis* on *P. gambelii* have not yet been investigated but might include competition, disease transmission, or differential susceptibility to fish predation, consistent with other crayfish species replacements (Lodge et al. 2000). Egly and Larson (2018) also found *P. gambelii* to be commonly extirpated from historical sites where benthic habitat has been impaired by land-use change, which may be relevant at some locations within the Bear River drainage with more intensive agricultural or urban land cover. Conversely, we did find *P. gambelii* within several streams of southern Yellowstone National Park as previously reported by Dean et al. (1975). These populations may be particularly important to the long-term persistence of *P. gambelii* in Wyoming because they are within a protected area that is currently isolated from downstream populations of *F. virilis* in the Snake River drainage by dispersal barriers (i.e., dams).

We were surprised to discover new populations of *F. neglectus* and *F. rusticus* in drainages where these species were not historically documented. *Faxonius neglectus* was known from isolated locations in the South Platte River drainage of far southeastern Wyoming as of Hubert's 1988 and 2010 surveys, but we found an expanded distribution in 2020 that included sites within the North Platte and Niobrara River drainages. This finding is consistent with Schainost (2011), who found *F. neglectus* to be more common throughout these same river drainages in Nebraska than was previously known. *Faxonius neglectus* may be a native species expanding its range in response to factors like climate or land-use change (e.g., Rhoden et al. 2016a, Dunn et al. 2021). However, because of its lack of presence in downstream reaches, we surmise that its movement into the North Platte drainage was likely facilitated by human-mediated transport (e.g., bait bucket transfer). We caution that *F. neglectus* is an invasive species in both the northeastern (Daniels et al. 2001) and northwestern USA (Pearl et al. 2013), and this crayfish has been documented to replace native species as it spreads (Larson et al. 2009).

We also discovered the highly invasive *F. rusticus* in new locations within the North Platte River drainage of Wyoming from 2016 to 2020. Previous discoveries of *F. rusticus* in Wyoming were attributed to stocking of private ponds for fisheries management, and these populations were believed to be eradicated by management interventions (WGFD 2010, 2021). Our discovery of *F. rusticus* in new locations suggests that introduction of this species to Wyoming was either more widespread than originally realized or is ongoing through a variety of potentially unidentified invasion vectors or pathways (Lodge et al. 2000, DiStefano et al. 2009, Chucholl

2013). Management of these newly discovered *F. rusticus* populations may be difficult, although Messenger and Olden (2018) modeled potential to slow the spread of *F. rusticus* through removal or control of this species in rivers of western North America. Negative ecological effects of *F. rusticus* on native species and assemblages are well documented, though research in western North America is limited (Lodge et al. 1994, Olden et al. 2011, Twardochleb et al. 2013).

Multispecies occupancy models

The most pronounced change we found in Wyoming crayfish assemblages over time was *F. virilis*' replacement of *F. immunis* as this state's most commonly detected crayfish species. Bovbjerg (1970) found that *F. virilis* was competitively dominant over *F. immunis* in permanent waters, whereas *F. immunis* persisted in intermittent or ephemeral habitats because of its superior burrowing ability and tolerance of low dissolved oxygen concentrations. Our multispecies occupancy models supported Bovbjerg (1970), with *F. immunis* less likely to occupy more permanent sites when *F. virilis* was present but unaffected by *F. virilis* at less permanent sites. This finding is consistent with past research on context-dependent competitive interactions between crayfish species. For example, Larson et al. (2009) found that an invasive population of *F. neglectus* was most likely to replace a rare, endemic crayfish in the Ozark Plateau at less permanent stream sites because of its superior burrowing ability and desiccation tolerance. Similarly, invasive *F. rusticus* replace native *F. virilis* from rock and cobble habitats in lakes of Wisconsin, USA, but *F. virilis* can persist on soft substrates that are less suitable to *F. rusticus* (Peters and Lodge 2013). Smith et al. (2019) found similar effects statewide in Michigan, USA, where native crayfishes shifted to less preferred fine or silty substrates in the presence of dominant *F. rusticus*. Context-dependent competition and coexistence patterns can provide management-relevant insights for organisms like freshwater crayfish (Olden et al. 2011, Peters and Lodge 2013). For example, we anticipate that *F. virilis* will not displace *F. immunis* from the entire state of Wyoming because *F. immunis* will continue to persist in more intermittent or ephemeral habitats.

Faxonius virilis is both native to Wyoming east of the Continental Divide and nonnative to Wyoming west of the Continental Divide. Across both its native and nonnative ranges, we found *F. virilis* to have become more common over time, with apparent effects to other crayfish species like *F. immunis* and *P. gambelii*. *Faxonius virilis* is a widespread but minimally studied invasive species throughout western North America, where it threatens endemic crayfish species in California, USA (Light et al. 1995), competes with endemic fishes for food (Carpenter 2005), and affects ecosystem processes like leaf-litter breakdown in streams that historically lacked crayfish (Moody and Sabo 2013). *Faxonius virilis* may also facilitate the establishment and spread of other

nonnative species, like the Burbot *Lota lota* (Linnaeus, 1758), by serving as a highly abundant prey resource (Klein et al. 2015, Klobucar et al. 2016). Our finding that this crayfish was more likely to occupy sites with warmer summer water temperatures and more detectable when sampling at higher water temperatures supports past physiological work on *F. virilis* as a warmwater species (Wetzel and Brown 1993, Westhoff and Rosenberger 2016). Accordingly, many cooler, high-elevation sites may resist *F. virilis* invasions at present (see also Van Mierlo et al. 2022), but vulnerability to crayfish invasion may change over time because of climate change (Capinha et al. 2013, Dunn et al. 2021). Contrary to Light et al. (1995), we did not find a relationship between poor quality or degraded sites and *F. virilis* occupancy, perhaps because we modeled a combination of native and nonnative populations for this species rather than only nonnative populations whose establishment may be facilitated by habitat change. Finally, despite its prevalence as a nonnative species throughout western North America, ecological effects of *F. virilis* have not been as well studied as other invasive crayfishes like *F. rusticus* (Twardochleb et al. 2013, but see James et al. 2016). Future work might include mechanistic laboratory or mesocosm experiments to better understand ecological interactions between *F. virilis* and crayfishes like *F. immunis* or *P. gambelii* (Carpenter 2005, Hale et al. 2016) or could investigate patterns of assemblage and ecosystem change before and after *F. virilis* invasion in comparison with uninvaded control sites (Wilson et al. 2004, Jackson et al. 2014).

We found that few of our environmental predictors affected our ability to detect *F. immunis* or *F. virilis*. Water temperature at time of sampling was an exception, with *F. virilis* detection probability strongly increasing with increasing water temperatures. Sampling at temperatures >15°C would maximize probability of detecting this species. Our findings that mean annual discharge was not included as a detection probability predictor and that stream slope had only weak effects on detection probability for *F. virilis* suggest that our geographic information system-derived predictors may have been too coarse relative to field conditions affecting crayfish detection probability. Our finding that water temperature at time of sampling had a weak effect on *F. immunis* detection probability was unexpected and could warrant further research. However, because we detected *F. immunis* at 28/125 active search sites (22.4%) and *F. virilis* at 52/125 active search sites (41.6%), we do not believe we were underpowered to model either occupancy or detection probability for these species in multispecies occupancy models (Rota et al. 2016).

Limitations and future research

Our study has several limitations that could be improved upon in future work. First, in the multispecies occupancy models, we used model occupancy of 1 species conditional on the presence or absence of a 2nd species, but we did not

infer that 1 species is dominant over the other (Rota et al. 2016). Our inferences of *F. virilis* dominance over *F. immunis* are supported by other experimental and observational work with these species (Bovbjerg 1970, Hale et al. 2016, James et al. 2016) but would be strengthened by additional modeling or experimental studies. Another limitation of our occupancy models is that we mixed lotic and lentic ecosystems in our models. To maintain the highest possible sample size, we chose to model lotic and lentic sites together, which necessitated adapting some lotic environmental covariates for lentic ecosystems (Hill et al. 2016). Higher sample replication in the future may allow a focus on lotic and lentic ecosystems separately, which might recover additional context-dependent patterns of crayfish occupancy and coexistence (Olden et al. 2011, Peters and Lodge 2013, Smith et al. 2019).

With respect to trends in crayfish assemblage composition over time, we acknowledge that crayfish species may differ in their detectability to different sampling gear (Larson and Olden 2016). Accordingly, some increases or decreases in apparent prevalence from our earlier to later time periods could be caused by a shift from opportunistic collection with fish sampling in Hubert (1988) to active sampling for crayfish in later surveys. Future surveys for crayfish assemblages in Wyoming could be improved by standardized sampling methodologies and data reporting (including absences) at resampled sites stratified across drainages. Some crayfishes, like *F. immunis* or *L. nebrascensis*, might also be more detectable in spring or early summer prior to burrowing in response to drying habitats (Rhoden et al. 2016b), and future surveys for these species might prioritize sampling early in the year.

We evaluated change in Wyoming's crayfish assemblages over time using a variety of data sources with different sampling methods and reporting practices, including the occasional omission of absence data. Despite these limitations, we believe we have documented real, management and conservation-relevant changes to Wyoming crayfish assemblages over time. In addition, our approach of using heterogeneous data sources to study temporal trends is common for many ecological communities (Olden et al. 2006, Peters et al. 2014). We hope our study provides a rigorous baseline for ongoing monitoring of Wyoming's crayfish assemblages, supporting future insights into both patterns and processes of increasing or decreasing prevalence of species (Olden et al. 2011, Smith et al. 2019).

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conceptualization, methodology, investigation, data curation, review and editing of the manuscript, supervision, project administration, and funding acquisition.

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