Freshwater Biology WILEY

Species traits predict stream-fish invaders in an Appalachian (U.S.A.) river basin

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Abstract

1. We compared the influence of biological traits (morphology, physiology, reproduction, and life history), ecological traits (geographic distribution, habitat associations, food habits), and introduction attributes (propagule pressure, human use of a species, residence time) on invasion success of native and introduced stream fishes during the colonisation and spread stages in an Appalachian (U.S.A.) river basin.

2. Colonisation success was positively related to residence time, benthic feeding, an equilibrium life-history strategy, and nest spawning. Successful spread was associated with tolerance to increased temperature and an equilibrium life-history strategy. The spread of introduced fishes was negatively related to gamefish status. No effect of propagule pressure was detected.

3. Traits linked to invasion success were consistent with the hypothesis that human land-use practices increase the invasibility of highland catchments by creating novel conditions better suited to lowland and equilibrium invaders.

4. We found biological traits to be more useful than ecological traits in predicting invasion success and suggesting invasion mechanisms. Parental care and nest association can facilitate invasions over large spatial extents for both native and introduced fishes. Analyses of suites of traits can reveal mechanisms of invasions and tactics for controlling them; such mechanisms and tactics may be system-specific and scale-dependent.

KEYWORDS
colonisation, equilibrium life history, invasive species, nest spawning, spread

1 | INTRODUCTION

Species invasion comprises four stages: transport; colonisation; establishment; and spread (Theoharides & Dukes, 2007; Williamson, 1996). Each stage presents a would-be invader with distinct ecological filters or barriers that limit the species proceeding to the next stage (Figure S1; Blackburn et al., 2011; Richardson et al., 2000). As an invasion progresses, its spatial extent generally increases; however, human-assisted invasions can occur faster and more extensively than invasions relying solely on natural processes (Theoharides & Dukes, 2007). Establishment is the most studied stage for fish invasions, but few studies address stages before and after establishment (García-Berthou, 2007). Although invasion biology typically focuses on introduced species, native species can also be invaders (Jones, Helfman, Harper, & Bolstad, 1999; Scott & Helfman, 2001); thus, principles of invasion also apply to native species.

A successful invasion requires a match between an invader's traits and the receiving environment (Bomford, Barry, & Lawrence, 2010).

Invader traits interacting with ecological filters (Poff 1997), often mediated by human activities, define the invadeable area for a given species across a given landscape (Catford, Jansson, & Nilsson, 2009; Peterson et al. 2011; Figure S2). In short, given access to a new area, an invader can occupy areas where biotic and abiotic conditions are suitable and essential resources are accessible. The specific traits, filters, and human factors driving invasion success may differ among stages (Kolar & Lodge, 2001; Kolar & Lodge, 2002; Marchetti, Moyle, & Levine, 2004; Theoharides & Dukes, 2007; Vermeij, 1996; Figure S1). These system- and stage-specific drivers underscore the need for basic knowledge of which traits lead to successful invasions in which environmental contexts. Such knowledge can reveal potential ecological consequences of invasion and promote more pragmatic and effective management approaches.

Fishes possess biological (morphology, reproduction, physiology, and life-history) and ecological (trophic, geographic distribution, and habitat preference) traits (Frimpong & Angermeier, 2010). *Biological traits* reflect innate (independent of the proximate environment) physiological requirements and morphological and life-history adaptations that have evolved over long time-scales (Frimpong & Angermeier, 2010; Vieira et al., 2006). These traits can provide mechanistic explanations for a species' response to the environment but may be phylogenetically constrained (Poff et al., 2006). To derive such explanations, one approach is to focus on the biological traits that drive behaviours, while accounting for species' relatedness (i.e. phylogeny; Frimpong & Angermeier, 2010). A life-history strategy comprises multiple biological traits that mediate trade-offs among an individual's survival, growth and reproduction (Winemiller, 2005; Winemiller & Rose, 1992). Winemiller and Rose (1992) (hereafter, the W&R model) recognised three strategies representing endpoints along gradients of fish life-history traits: opportunistic, periodic, and equilibrium (Figure S3). Presumably, these strategies differ in their propensity to facilitate invasion success in any given environmental context.

Ecological traits reflect an organism's preferences and behaviours (Vieira et al., 2006), and are therefore indirect expressions of biological traits (Frimpong & Angermeier, 2010). Ecological traits are more sensitive than biological traits to the proximate environment, and less strongly linked to phylogeny, but can be tautological when used to test a species' response to the same environmental factors used to define an ecological trait (Poff et al., 2006; Vieira et al., 2006).

Human factors related to introduction pathways, purpose, and effort (i.e. introduction attributes) directly affect invasion success. Propagule pressure (the product of individuals released and number of release events; Lockwood, Cassey, & Blackburn, 2005) is a key invasion driver (Catford et al., 2009; Marchetti et al., 2004). Since human preferences largely dictate which species are introduced (or not) and mediate propagule pressure, predictors related to human uses of species (e.g. sport, bait, or aquarium) can influence invasion success (Alcaraz, Vila-Gispert, & García-Berthou, 2005; Davis & Darling, 2017; Peoples & Midway, 2018; Ruesink, 2005). Since invasion rates and drivers (e.g. propagule pressure and population growth) vary temporally, an invader's residence time since introduction into a new area may predict invasion success (Barney & Whitlow, 2008; Catford et al., 2009; Ruesink, 2005; Scott & Panetta,

1993; Vila-Gispert, Alcaraz, & García-Berthou, 2005 but see Kolar & Lodge, 2001, 2002).

Humans also regulate invasions indirectly through changes to ecological filters. For example, invasions by native or introduced species alike into previously unsuitable areas may be facilitated by formation of novel anthropogenic conditions such as impoundments (Lapointe, Thorson, & Angermeier, 2012; Olden, Poff, & Bestgen, 2006) and deforestation (Lorion & Kennedy, 2009; Scott & Helfman, 2001). Landscape-scale alterations have transformed mountain streams such that they possess key attributes of lowland streams (increased water temperature, fine sediment, nutrients, and lentic habitat) (Jones et al., 1999). These evolutionarily novel conditions favour generalist, silt-tolerant, warmwater species, including non-natives, as well as natives previously restricted to downstream reaches (Angermeier & Winston, 1998; Scott & Helfman, 2001).

Prior analyses of invader traits have taught us to address invasion stages independently, consider introduction attributes, and control for inter-dependence among species (Catford et al., 2009; García-Berthou, 2007; Gido & Brown, 1999; Kolar & Lodge, 2002; Lockwood et al., 2005; Marchetti et al., 2004; Ruesink, 2005). In a global synthesis of fish invasiveness studies, García-Berthou (2007) identified five pressing research needs: (1) investigation of invasion stages other than establishment; (2) more precise measures of propagule pressure; (3) studies from additional geographic regions; (4) comparisons of native and introduced species; and (5) analyses based on comprehensive datasets of species traits. Furthermore, we note that prior invasiveness studies comparing natives to non-natives, or successful versus failed non-native invaders, have overlooked within-in-drainage native invasions, which can provide an early indication of ecological impairment (Scott & Helfman, 2001) and bolster sample sizes in analytical models of invasion success.

Herein, we examined species traits and introduction attributes of 74 fish species (native and introduced) in tributaries of the New River basin (central Appalachian Mountains, U.S.A.) during colonisation and spread stages. We addressed the needs identified above while investigating the following questions: (1) Do strong colonisers and spreaders share traits that consistently differentiate them from weak colonisers and non-spreaders? (2) Do influential species traits differ between colonisation and spread stages? (3) How important are introduction attributes (propagule pressure, residence time, game/non-game status) compared to biological and ecological species traits in influencing invasion outcomes? We then interpreted how our trait-based analyses informed our view of dominant ecological filters shaping fish communities.

2 | METHODS

2.1 | Study area and fauna

The study area included tributaries (but not the mainstem) of the upper and middle sub-basins of the New River basin of North Carolina and Virginia, U.S.A. (hereafter UMNR, Figure 1), which

drains approximately 10,000 km^2 of the Blue Ridge, and Valley and Ridge ecoregions (Omernik, 1987). These two sub-basins have the highest average elevation (829 and 764 m above sea level, respectively) of Virginia's 39 sub-basins. The New River basin has been intensively used since the 1750s. Land cover currently comprises 63% forest, 28% agricultural, and 7% developed lands (Fry et al., 2011; Figure 1). Five hydroelectric dams on New River and one on the largest UMNR tributary, Little River (Virginia), were constructed from 1902 to 1939 (Figure 1). The large impoundments behind these dams, along with over 1,600 smaller impoundments intersecting the UMNR stream network (Simley & Carswell, 2009), have been repeatedly stocked with non-native game and prey fishes over the past century.

Due to its montane aspect, south-to-north orientation, and large natural falls at the outlet, the New River basin has the lowest native fish species richness (44) of all 26 major drainages in the eastern U.S.A., including nine endemics (Jenkins & Burkhead, 1994). State-sanctioned stockings of non-native game and prey species, especially from the mid-1800s to the 1970s, supplemented by continuing unauthorised introductions, have contributed at least 55 established introduced fish species, such that the basin has the greatest ratio of introduced-to-native species (55:44, Buckwalter, Frimpong, Angermeier, & Barney, 2018) among eastern U.S.A. drainages (Jenkins & Burkhead 1994; Peoples, Midway, DeWeber, & Wagner, 2017).

These natural and anthropogenic factors make the UMNR a particularly rich system for the study of stream-fish invasions in a region underrepresented in the invasion literature and offer a basis for understanding fish invasions in other montane, temperate river basins worldwide.

2.2 | Fish traits and introduction attributes matrix

We compiled a matrix of UMNR species traits (Table 1) based primarily on the FishTraits database (Frimpong & Angermeier, 2009; Jenkins & Burkhead 1994; and other sources (Table S1). Traits were categorised as biological or ecological. All seven trait domains defined by Frimpong and Angermeier (2010) were represented. We also compiled introduction attributes describing propagule pressure (INTROEFF), residence time (FIRSTREC), and human use (GAME). We removed highly correlated variables (Pearson or Spearman's $r \geq$ 0.8; Table S1), keeping the most parsimonious variable (e.g. algae or phytoplankton feeder was retained rather than herbivore or diet breadth when all three were highly correlated), or the variable that was available for more species.

2.3 | Accounting for phylogenetic correlation in biological traits

Since closely related species share biological traits due to common ancestry, we first accounted for phylogenetic non-independence of biological
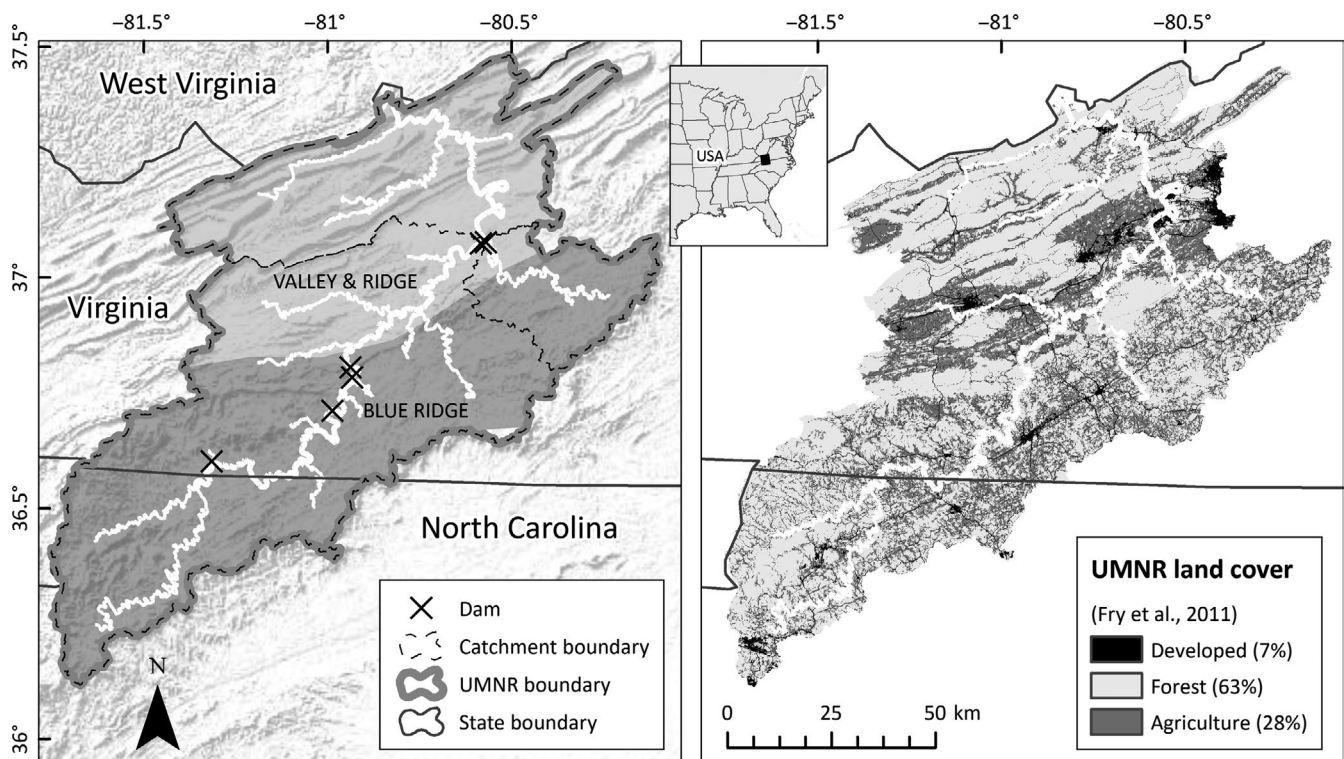

FIGURE 1 The upper and middle New River (UMNR) study area comprised the Virginia and North Carolina portions of the New River basin. Left map shows physiographic provinces and major dams. Right map shows 2006 land cover *sensu* Fry et al. (2011). Adapted from Buckwalter et al. (2018)

TABLE 1 List of compiled fish species traits and introduction attributes

Domain	Trait	Description	Data type
Biological traits			
Life history	AGE1REPRO	Typical age at first reproduction (years)	Numeric
	LEN1REPRO	Lower limit of typical adult length range (total length, mm)	Numeric
	FECUNDITY	Maximum reported fecundity (egg count)	Numeric
	LONGEVITY	Longevity in the wild (years)	Numeric
	GENTIME	Average age of parents at the time their young are hatched/born	Numeric
	PERIOD_D	Distance in multivariate trait space between each species' position and Winemiller and Rose (1992) life history vertex; smaller distances indicate greater affiliation with a given vertex	Numeric
	EQUIL_D		Numeric
	OPPORT_D		Numeric
Morphology	MAXTL	Maximum total length (mm) reported from Virginia, if available; otherwise, a record from a neighbouring state was used	Numeric
	MTHANG	Mandible angle on a scale from −1 (inferior) to +1 (superior)	Numeric
	MTHPOS	Mouth position on a scale from −1 (inferior) to +1 (superior)	Numeric
	RELEYEDIA	Horizontal eye diameter/total length (mm/mm)	Numeric
	RELMANLEN	Mandible length/total length (mm/mm)	Numeric
	SHPFACT	Total length/maximum body depth (mm/mm)	Numeric
	SWMFACT	Depth of the caudal peduncle/maximum caudal fin depth (mm/mm)	Numeric
Reproduction	PC	Degree of parental care: 0 = open-substrate spawner; 1 = brood hider; 2 = guarder or strong *Nocomis* nest associate; 3 = bearer	Ordinal
	SEASON	Length of spawning season (months, precision = 0.25)	Numeric
	SERIAL	Serial/batch spawner	Binary
	TIMING	Spawning starts in (1) April–September versus (0) October–March	Binary
	TSPAWNMIN	Minimum spawning temperature (C)	Numeric
Physiology	TMIN_JAN	Average minimum January air temperature (C) at native range centroid	Numeric
	TMAX_JUL	Average maximum July air temperature (C) at range centroid	Numeric
Ecological traits			
Geographic distribution	AREAKM2	Size of native range (km^2)	Numeric
	LATCEN	Latitude of native range centroid (decimal degrees)	Numeric
	LATMIN	Minimum latitude of native range (decimal degrees)	Numeric
	LONCEN	Longitude of native range centroid (decimal degrees)	Numeric
Habitat preference	PREFLOT	Prefers lotic systems	Binary
	SLOWCURR	Prefers slow current	Binary
	CREEK	Prefers creeks	Binary
	LARGERIV	Prefers medium to large rivers	Binary
	LOWLAND	Prefers lowland elevation	Binary
	MONTANE	Prefers mountainous physiography	Binary
	PHYSIOBRE	Total number of preferred physiography types	Ordinal
	WATBRE	Total number of preferred waterbody types	Ordinal
	LITHOPHIL	Rock, gravel, or sand spawner	Binary
Trophic	BENTHIC	Benthic feeder	Binary
	SURWCOL	Surface or water column feeder	Binary
	ALGPHYTO	Eats algae, phytoplankton	Binary
	FSHCRCRB	Eats fishes, crayfishes, crabs, frogs	Binary
	EGGS	Eats eggs of fishes, frogs, etc.	Binary

TABLE 1 (Continued)

Domain	Trait	Description	Data type
Introduction attributes			
	FIRSTREC	Year species was first detected in the New River drainage	Numeric
	INTROEFF	Introduction effort: estimated total number of individuals released in the New River basin since European settlement: (a) <100; (b) 100–1,000; (c) >1,000	Ordinal
	GAME	Commonly used by humans as gamefish, baitfish, or commercially	Binary

Note: Data sources are listed in Table S1.

traits among species (Alcaraz et al., 2005; Felsenstein, 1985; Fisher & Owens, 2004). We used phylogenetic eigenvector regression (Diniz-Filho, Ramos de Sant'Ana, & Bini, 1998), which accommodates small sample sizes, low phylogenetic correlation, varying data types, and phylogenetic uncertainty better than other methods (Diniz-Filho et al., 1998; Olden et al., 2006). Appendix S1 provides additional methodological details. Ecological traits were not subjected to phylogenetic eigenvector regression.

2.4 | Contribution of species traits to invasion outcomes

We defined two binary response variables, *Coloniser* and *Spreader*, to represent invasion success at two stages. *Coloniser* represented invasion success through the colonisation stage and applied only to the 39 introduced species. We defined colonisation success in terms of each species' contemporary distribution across three isolated UMNR catchments (Figure 1, left side), which we delineated by aggregating contiguous sixth-level hydrologic units (HUs; Simley & Carswell, 2009). Two upstream catchments (one upstream of Claytor Dam, completed on the New River in 1939, and the other upstream of Little River Dam, completed in 1934) were each isolated from the downstream catchment (downstream of Claytor Dam) by a major dam and reservoir such that natural movement by fishes between catchments was impossible in the upstream direction and highly unlikely in the downstream direction. Thus, occurrence in multiple catchments of a species introduced after dam completion required multiple human-aided colonisation events. Introduced species reported from <3 catchments were classified as weak colonisers; species reported from three catchments were strong colonisers. We summarised species occurrence by catchment based on Buckwalter et al. (2018) (Frimpong, 2017).

Spreader represented invasion success during the spread stage, and applied to the complete pool of 74 introduced and native UMNR species. We adopted Buckwalter et al.'s (2018) classification of spreaders and non-spreaders, which was based on temporal trends in *detections per HU sampled* (DPHS) in the UMNR since 1938, where DPHS was defined as the number of HUs a species was detected in per defined sampling period, divided by the total number of HUs sampled during the period. Herein, species that Buckwalter et al. (2018) classified as spreaders were assigned *Spreader* = 1; other species were assigned *Spreader* = 0.

We used boosted classification trees (BCT) to identify species traits that explained *Coloniser* and *Spreader* status. We initially

developed six BCT models: (1) *Coloniser* against biological traits; (2) *Coloniser* against ecological traits; (3) *Coloniser* against combined biological and ecological traits; (4) *Spreader* against biological traits; (5) *Spreader* against ecological traits; and (6) *Spreader* against combined biological and ecological traits. Introduction attributes were included in all six models to evaluate the influence of human preferences and invasion history on the responses. However, since GAME was the only introduction attribute that could be used in *Spreader* models based on the complete UMNR species pool (INTROEFF and FIRSTREC were not applicable to UMNR natives), we also developed a seventh model of *Spreader* against biological traits of introduced species only to enable comparison of effects of all three introduction attributes with effects of biological traits on the *Spreader* response.

We computed BCT models for *Coloniser* and *Spreader* with R statistical software (R Core Team, 2014) using the *dismo* package (Hijmans, Phillips, Leathwick, & Elith, 2015). Models were tuned following Elith, Leathwick, and Hastie (2008) to minimise predictive deviance and maximise area under the receiver operating characteristic curve (AUC) from 10-fold cross-validation. Additional details about BCT, along with model tuning settings, are in Appendix S1. Formulae developed by Friedman (2001) and implemented in *dismo* estimate the relative influence (%) and partial effect of each trait on the response. Relative influence is based on how often a trait was used for splitting (i.e. partitioning weak versus strong colonisers, and non-spreaders versus spreaders), along with the improvement to the model as a result of each split, averaged over all trees. Partial dependence plots provide a basis for interpreting the effect of each trait on the response, after accounting for the average effects of all other variables in the model (Elith et al., 2008). Finally, for a comprehensible model with a clear graphical representation to aid in interpreting trait interactions, we generated an individual classification tree model for each response using the predictors from the final BCT model. We built these individual models with the *rpart* package (Therneau, Atkinson, & Ripley, 2014) in R, using 10-fold cross-validation to identify optimal pruning.

3 | RESULTS

Boosted classification trees models for *Coloniser* and *Spreader* performed equivalently in terms of AUC scores (Table 2). Models based on biological traits had higher AUC scores than those based on ecological traits. Models with ecological and biological traits combined performed

TABLE 2 Mean cross-validated area under the receiver operating characteristic curve (followed by *SE*) for boosted classification tree models of binary *Coloniser* and *Spreader* responses for fishes occurring in upper and middle New River tributaries

Trait type	Response		
	Coloniser (*n* = 39 introduced spp.)	*Spreader* (*n* = 74 introduced and native spp.)	*Spreader* (*n* = 39 introduced spp.)
Biological	0.793 (0.053)	0.790 (0.042)	0.825 (0.084)
Ecological	0.660 (0.102)	0.648 (0.067)	—
Combined	0.820 (0.064)	0.755 (0.032)	—

Note: Model tuning settings are in Appendix S1

no better than models based solely on biological traits. For clarity and brevity, we present results for only the most influential traits in each model (i.e. traits having relative influence ≥5%; Table 3; Figure 2).

3.1 | Coloniser traits and introduction attributes

3.1.1 | Biological traits

Twelve biological traits and one introduction attribute (FIRSTREC) were retained in the final BCT model for *Coloniser* (Table 3). Strong colonisers were introduced earlier (FIRSTREC, relative influence = 21.6%), had smaller eyes relative to body length (RELEYEDIA, 14.5%), provided more parental care (PC, 13.8%), adopted a less opportunistic life-history strategy (OPPORT_D, 8.9%), or had a more ventral mouth position (MTHPOS, 7.8%) or angle (MTHANG, 7.2%) than weak colonisers (Figure 2a). All 12 species introduced before 1940 were classified as strong colonisers, whereas all five species introduced after 1985 were weak colonisers. Ten of 12 (83%) weak colonisers (along with five of 27 [19%] strong colonisers) exhibited a combination of low PC and high RELEYEDIA (Figure 3a). Indicators of game/non-game status (GAME) and propagule pressure (INTROEFF), along with both physiology traits (TMIN_JAN and TMAX_JUL), were not informative in the *Coloniser* model.

3.1.2 | Ecological traits

Nine ecological traits and two introduction attributes remained in the final BCT model for *Coloniser* (Table 3). Strong colonists tended to be introduced before 1940 (FIRSTREC, 37.2%), had a native range centroid ≥36°N (LATCEN, 25.5%), or had a southern native range limit >27°N (LATMIN, 14.1%; Figure 2b). Most (25 of 27 [93%]) strong colonisers, along with six of 12 (50%) weak colonisers, were either first detected before 1940 or had LATCEN ≥36°N (Figure 3b). Four of the five (all except FIRSTREC) most influential ecological traits in the BCT for *Coloniser* described geographic distribution.

3.2 | Spreader traits and introduction attributes

3.2.1 | Biological traits

Three biological traits remained in the final *Spreader* model based on the complete species pool (introduced + native species; Table 3). Spreaders tended to be adapted to warmer winters (TMIN_JAN, 38.6%), or were equilibrium W&R strategists as indicated by reduced EQUIL_D (33.2%) and body length at onset of maturity (LEN1REPRO, 28.2%; Figure 2c). Most (34 of 43 [79%]) non-spreaders (along with seven of 31 [23%] spreaders) exhibited a combination of high EQUIL_D and low TMIN_JAN (Figure 3c). To further interpret effects of individual life-history traits on *Spreader*, we reran the BCT with W&R strategies EQUIL_D, OPPORT_D, and PERIOD_D excluded. With AUC = 0.743 (*SE* = 0.051), this rerun approached the accuracy of the full model (0.790, *SE* = 0.042, Table 2) and suggested that the importance of EQUIL_D was mediated by a shorter spawning season (SEASON, 20.8%) and greater PC (19.8%).

GAME was the only introduction attribute applicable to *Spreader* models for the full UMNR species pool, but it did not appear in any final *Spreader* model (Figure 2c,d). When the *Spreader* model was rerun on only the introduced species, with all three introduction attributes included, *FIRSTREC* and *INTROEFF* were non-informative. However, *GAME* entered the model as the second-most influential predictor (Table 2, Figure 2e) and was negatively related to spread (i.e. a smaller proportion of game species were classified as spreaders than non-game species). TMIN_JAN and EQUIL_D had similar effects on *Spreader* as in the full model.

3.2.2 | Ecological traits

Ten ecological traits remained in the final BCT model for *Spreader* (Table 3). Spreaders tended to have LATCEN (32.8%) <37°N, native range area (AREAKM2, 24.6%) <1.4 × 10⁶ km², LATMIN (15.0%) >35°N, longitude of their native range centroid (LONCEN, 9.8%) ≤79°W, or to avoid eating algae or phytoplankton (ALGPHYTO, 8.1%; Figures 2d and 3d). Most (42 of 43 [98%]) non-spreaders (along with 14 of 31 [45%] spreaders) either had AREAKM2 ≥1.4 × 10⁶ km², or their native range centroid was located north of 37°N or west of 79°W (Figure 3d). As was the case for *Coloniser*, four of the five most influential ecological traits for *Spreader* described species' geographic distributions. LATMIN was positively related to both *Coloniser* and *Spreader*; however, LATCEN, AREAKM2, and LONCEN had opposing effects on the two responses.

4 | DISCUSSION

Rigorous assessments of relations among species traits, environmental contexts, and invasion success are difficult because (1) species success varies among invasion stages, (2) the human factors and ecological filters at play vary among invasion cases, and (3) stage-specific information on species' occurrence is typically sorely incomplete. Invasion

Biological trait	Response			Ecological trait	Response	
	Coloniser	Spreader			Coloniser	Spreader
	(I only)	(I + N)	(I only)		(I only)	(I + N)
EQUIL_D	2.9	−33.2	−42.8	FIRSTREC*	−37.2	NA
TMIN_JAN	—	+38.6	+20.2	LATCEN	+25.5	−32.8
LEN1REPRO	3.7	−28.2	-	AREAKM2	+7.9	−24.6
FIRSTREC*	−21.6	NA	—	LATMIN	+14.1	+15.0
GAME*	—	—	−21.3	LONCEN	−5.7	+9.8
SEASON	—	—	−15.7	ALGPHYTO	1.1	−8.1
RELEYEDIA	−14.5	—	—	INTROEFF*	3.9	NA
PC	+13.8	—	—	SURWCOL	—	2.6
OPPORT_D	+8.9	—	—	FSHCRCRB	2.2	—
MTHPOS	−7.8	—	—	PREFLOT	0.7	2.1
MTHANG	−7.2	—	—	MONTANE	1.1	1.9
FECUNDITY	−5.6	—	—	SLOWCURR	—	1.6
SWMFACT	−5.3	—	—	LOWLAND	—	1.4
SERIAL	4.2	—	—	EGGS	0.6	—
PERIOD_D	2.5	—	—	BENTHIC	—	—
SHPFACT	2.0	—	—	CREEK	—	—
AGE1REPRO	—	—	—	GAME*	—	—
GENTIME	—	—	—	LARGERIV	—	—
INTROEFF*	—	NA	—	LITHOPHIL	—	—
LONGEVITY	—	—	—	PHYSIOBRE	—	—
RELMANLEN	—	—	—	WATBRE	—	—
TIMING	—	—	—			
TMAX_JUL	—	—	—			
TSPAWNMIN	—	—	—			

TABLE 3 Relative influence (%) of introduction attributes (marked with an *) and species traits (Table 1) of fishes occurring in upper and middle New River tributaries (I = 39 introduced species, N = 35 native species) in boosted classification tree models for binary *Coloniser* and *Spreader* responses

Note: Columns 2–4 show the influence of *biological* species traits and introduction attributes; columns 6–7 show the influence of *ecological* species traits and introduction attributes. Introduction attributes *FIRSTREC* and *INTROEFF* applied only to introduced species, and therefore were not applicable (NA) in the full (I + N) *Spreader* models (columns 3 and 7). To enable a comparison of effects of all three introduction attributes, along with biological traits, on the *Spreader* response, the *Spreader* model was rerun for introduced species only (column 4). Traits contributing >5% to the response are shown in bold; their relative influence values are prefixed with + or − to indicate whether the trait was positively or negatively, respectively, related to the response, based on the overall trend in the partial dependence plot (Figure 2). Traits are listed in descending order by their maximum relative influence across both responses. — indicates redundant/non-informative traits that were dropped from the final simplified models.

studies commonly identify (retrospectively) which species traits best explain success and/or failure, but accounting for potential confounding factors is often problematic. For example, several studies have examined associations between fish traits and transport or colonisation success by comparing the pool of detected introduced species to a pool of undetected species from some donor region (Colautti, 2005; Duggan, Rixon, & MacIsaac, 2006; Jeschke & Strayer, 2006). Interpretation of such studies is limited by uncertainty regarding which introductions have been attempted (García-Berthou, 2007) and how to define the pool of undetected species (Vermeij, 1996). Our analytical approach minimised these uncertainties by comparing traits of strong versus weak colonisers in a recipient region after detection. Thus, we assessed a species' success in the transport and colonisation stages combined.

Measures of fish invasion success during the spread stage typically focus simply on the number of waterbodies invaded by introduced species (Kolar & Lodge, 2002; Marchetti et al., 2004; Ribeiro, Elvira, Collares-Pereira, & Moyle, 2008; Vila-Gispert et al., 2005). However, this approach ignores temporal variation in sampling effort and the possibility that the extant environmental filters also promote concurrent invasions by native species. Our approach minimised these biases by analyzing both native and introduced species and by accounting for temporal variation in sampling effort.

Biological traits

(a)

FIRSTREC (21.6%)

RELEYEDIA (14.5%)

PC (13.8%)

OPPORT_D (8.9%)

MTHPOS (7.8%)

MTHANG (7.2%)

Effect on Coloniser

Ecological traits

(b)

FIRSTREC (37.2%)

LATCEN (25.5%)

LATMIN (14.1%)

AREAKM2 (7.9%)

(c)

TMIN_JAN (38.6%)

EQUIL_D (33.2%)

LEN1REPRO (28.2%)

Effect on Spreader

(e)

EQUIL_D (42.8%)

GAME (21.3%)

TMIN_JAN (20.2%)

SEASON (15.7%)

(d)

LATCEN (32.8%)

AREAKM2 (24.6%)

LATMIN (15%)

LONCEN (9.8%)

ALGPHYTO (8.1%)

4.1 | Traits influencing colonisation success

Biological traits associated with strong colonisers included smaller eyes (RELEYEDIA) and bottom-oriented mouth position (MTHPOS)

and angle (MTHANG), all of which may be linked in a benthic feeding strategy (Frimpong & Angermeier, 2010). However, mechanisms for how benthic feeding might enhance colonisation remain largely unexplored. The strong negative effect of RELEYEDIA on *Coloniser*
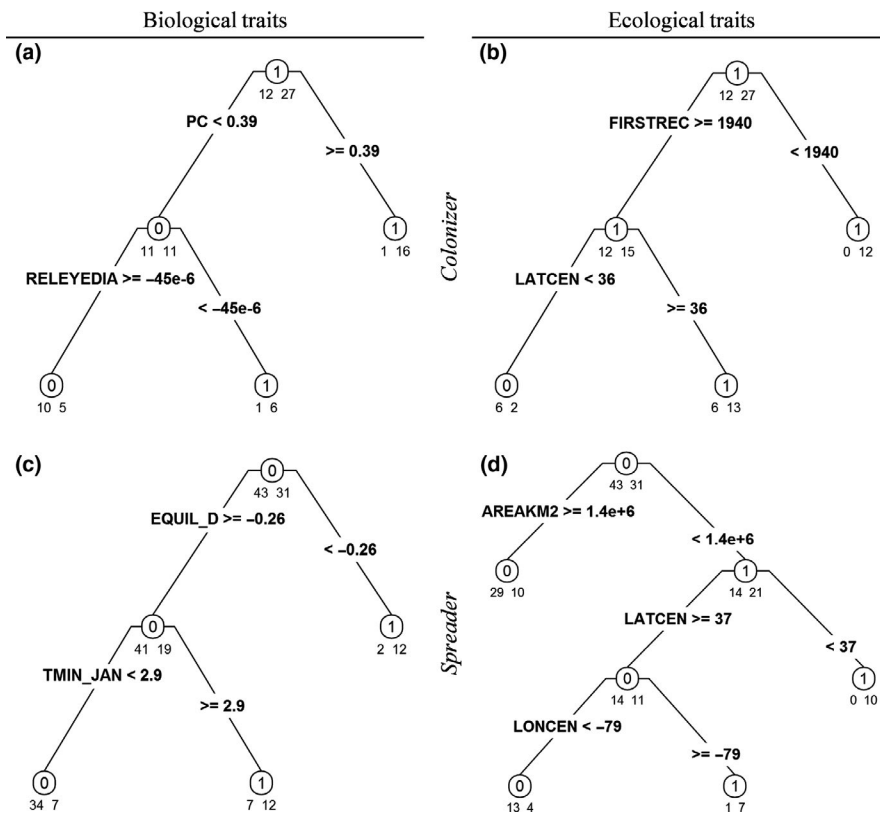
FIGURE 3 Optimally pruned classification trees for the contribution of biological (a, c) and ecological (b, d) traits (Table 1) of 39 introduced and 35 native fish species reported from tributaries of the upper and middle New River to responses of two binary variables, *Coloniser* (a, b) and *Spreader* (c, d). Labels inside nodes (circles) indicate the predicted response class (0 = weak coloniser/non-spreader, 1 = strong coloniser/spreader). Labels below nodes indicate the observed number of species in each response class (0, 1). Splits are labelled with the values of the trait that determined the split. Values of biological traits (a, b) represent residuals from phylogenetic eigenvector regression, and therefore are not on the same scale as the original measurements. *FIRSTREC* was an introduction attribute included in both analyses for *Coloniser*

suggests an adaptive disadvantage for visual feeders, perhaps due to the increased turbidity resulting from intensive land use. The interaction between RELEYEDIA and PC suggests that benthic feeding was particularly important to strong colonisers that provided less PC.

Strong colonisers' position in W&R space and their provision of PC suggests they typically adopt an equilibrium life-history strategy. By emphasising juvenile survival over egg production, equilibrium strategists fare better in relatively stable and/or chronically stressful environments, where the influence of biotic interactions surpasses that of stochastic abiotic disturbances in filtering species (Winemiller & Rose, 1992). Impoundments, which are more environmentally stable than rivers and favour fishes with equilibrium strategies (McManamay & Frimpong, 2015; Mims & Olden, 2013; Olden et al., 2006), are abundant in the UMNR. Moreover, impoundments are persistent sources of dispersers that colonise streams far beyond the impounded reaches (Havel, Kovalenko, Thomaz, Amalfitano, & Kats, 2015; Johnson, Olden, & Vander Zanden, 2008; Moyle & Light, 1996; Olden et al., 2006). However, given that the total surface area of lentic waterbodies is just 0.27% of the

UMNR area, it seems unlikely that impoundments alone explain the enhanced colonisation success of equilibrium species in UMNR streams.

Altered sediment dynamics may play a role in selecting successful colonisers (i.e. equilibrium strategists with high PC) in the UMNR, given that unsilted interstitial spaces in stream substrates are crucial for the persistence of many montane fishes (Berkman & Rabeni, 1987; Chapman et al., 2014; Sutherland, Meyer, & Gardiner, 2002). Intensive land use (e.g. deforestation, agriculture) accelerates fine sediment loading, thereby filling interstitial spaces (Jones et al., 1999; Scott & Helfman, 2001), and perhaps exacerbating competition for interstitial space/resources. Such chronic, widespread competition for a limiting resource generally favours equilibrium strategists.

Parental care seems to be the main driver of colonisation success for equilibrium strategists in the UMNR. Most (16 of 17) introduced species having PC ≥0.39 were strong colonisers. All 16 of these either build nests (14 species) or spawn in nests of host species (two species). Nest spawning enhances reproductive success in highly silted streams by providing unsilted substrate for egg and embryo survival (Peoples, Blanc, & Frimpong, 2015; Peoples, Tainer,

& Frimpong, 2011). Nest builders also frequently guard against egg predators or bury eggs for the same effect (Jenkins & Burkhead, 1994). If *Coloniser* represented colonisation success during the transport and colonisation stages per se, we would not expect a reproductive trait such as PC to be a strong predictor. Instead, this pattern suggests ecological filters may influence our *Coloniser* response during the establishment stage, perhaps because of a lag between colonisation and initial detection.

The ecological traits contributing to colonisation success (LATCEN, LATMIN, and AREAKM2) described the geography of species' native ranges. Latitude metrics reflect associations with climate, while range size reflects general physiological tolerance (Frimpong & Angermeier, 2009; Theoharides & Dukes, 2007). This pattern suggests an ecological filter that favours species adapted to cool waters and/or a broad temperature range. In general, widespread species are also more likely to be transported to new sites.

Biological traits were more reliable predictors of fish colonisation success in the UMNR than ecological traits. Our *Coloniser* model based on biological traits was more accurate than the ecological traits model (AUC from cross-validation = 0.79 and 0.66, respectively). The analysis using biological traits indicated greater support for the contribution of feeding morphology and life-history traits, rather than physiology/climate tolerance traits, to colonisation success. Ecological traits did not convincingly discriminate strong versus weak colonisers. Further, because ecological traits are indirect expressions of biological traits, the latter are expected to better explain observed ecological processes (Frimpong & Angermeier, 2010).

4.2 | Traits influencing spread success

The strong positive response of spreaders to TMIN_JAN is consistent with the facts that air temperatures are warming (Huang, Frimpong, & Orth, 2016) and air–water temperatures are tightly coupled (Erickson & Stefan, 2000). However, streams also warm because of intensive uses of catchments, such as deforestation, impoundments, water withdrawals, and stormwater runoff (Poole & Berman, 2001). Thus, multiple anthropogenic factors may be contributing to warming of the UMNR's streams, thereby facilitating invasions by warmwater species (Angermeier & Winston, 1998; Jones et al., 1999; Scott & Helfman, 2001).

UMNR spreaders, like colonisers, also tended toward an equilibrium life-history, as indicated by low values of EQUIL_D, a short spawning season, and PC (Winemiller, 2005). As was the case for traits associated with colonisation success, the ongoing spread of equilibrium species may signal a basin-wide shift toward greater environmental stability and/or chronic stress. Our leading candidate for a landscape filter capable of driving the expansion of equilibrium species, especially nest spawners, across the UMNR is the widespread, chronic accumulation of fine sediment in streams.

Similar to the case for *Coloniser*, ecological traits describing species' geography (i.e. LATCEN, AREAKM2, and LATMIN) were less predictive of spread success than biological traits (AUC = 0.648 and 0.790, respectively). Interestingly, colonisation increased with increasing LATCEN,

while spread decreased. These opposing effects suggest a transition in dominant ecological filters between invasion stages (Kolar & Lodge, 2001; Marchetti et al., 2004; Theoharides & Dukes, 2007; Vermeij, 1996). The positive effect of LATCEN on *Coloniser* may reflect the importance of climate matching during colonisation (Bomford et al., 2010; Theoharides & Dukes, 2007), whereas the negative effect on *Spreader* might demonstrate the ability of southern species to establish new populations in novel warmwater habitats created anthropogenically (Angermeier & Winston, 1998; Lapointe et al., 2012; Scott & Helfman, 2001).

No trophic trait except ALGPHYTO (herbivory) exhibited notable influence on spread. The inverse relationship observed between herbivory and spread may reflect competitive displacement of some herbivores by a few widespread algae-eaters. The three most abundant and widespread UMNR fishes, central stoneroller *Campostoma anomalum*, mountain redbelly dace *Chrosomus oreas*, and bluehead chub *Nocomis leptocephalus* (Buckwalter et al., 2018), are all avid algae-eaters (Jenkins & Burkhead, 1994).

None of the life-history traits (body size, longevity, delayed maturation, and fecundity) positively associated with global establishment of freshwater fishes outside their country of origin (Liu, Comte, & Olden, 2017), and also associated with establishment of eastern U.S.A. non-game species outside their native basin (Peoples & Midway, 2018), strongly predicted colonisation or spread in the UMNR. This discrepancy could partly reflect methodological differences (e.g. in invasion stages assessed or traits considered) between previous studies and ours. However, our contrasting results suggest that the spatial resolution at which invasions are viewed (i.e. sixth-level HU herein, fourth-level HU in Peoples & Midway 2018, and countries in Liu et al., 2017) can influence conclusions regarding invasion drivers.

4.3 | Influence of introduction attributes versus species traits in invasion outcomes

Time has been linked to successful fish invasions in later stages (Ruesink, 2005; Vila-Gispert et al., 2005), and to establishment of birds and plants (Kolar & Lodge, 2001), but ours is the first study to document a relationship between residence time (FIRSTREC) and colonisation success. Residence time was the strongest predictor of colonisation success in our biological and ecological traits models. Overall colonisation success declined after two distinct periods: *c.* 1940 and *c.* 1980. The first period followed construction of Little River Dam (1934) and Claytor Dam (1939), which isolated the three UMNR catchments and probably limited subsequent colonisation. The second period coincided with reductions in state-sponsored stocking of new gamefish species (Jenkins & Burkhead, 1994). Although residence time sometimes predicts invasion success, time itself cannot influence the invasion process; rather the apparent effect of time reflects temporal variation in rates and drivers of invasions (Catford et al., 2009).

In contrast to residence time, INTROEFF (propagule pressure) and GAME (gamefish status) did not bolster colonisation or spread of introduced fishes in our models. Rather, when the *Spreader* model

was rerun against biological traits and introduction attributes of the introduced subset of UMNR species, GAME strongly and negatively affected *Spreader*. This effect probably reflects a mismatch between the habitat requirements of introduced gamefishes and the habitat available throughout most of the UMNR. Most introduced gamefishes were selected to enhance fishing opportunities in impoundments and mainstem rivers, which are environmentally distinct from unimpounded montane tributaries and represent a small fraction of UMNR waters. Three introduced gamefishes not classified herein as spreaders (smallmouth bass *Micropterus dolomieu*, bluegill *Lepomis macrochirus*, and common carp *Cyprinus carpio*) were already well established in the UMNR prior to the 1930s (Buckwalter et al., 2018); therefore, their initial spread phase was not captured by our *Spreader* models. However, even if we group these gamefishes among the spreaders, the proportion of introduced gamefish classified as spreaders (10/23 = 43%) is still half that of introduced non-game species (13/16 = 81%), all of which had native ranges bordering the UMNR. Therefore, our results suggest that, when viewed at the basin scale, non-game fishes introduced from neighboring basins are more likely to spread than exotic introduced gamefishes, with salmonids as notable exceptions.

Our finding of greater prevalence of non-game than game spreaders in the UMNR provides a counter-example to a recent study linking recreational fishing pressure to the spread (defined as the number of fourth-level HUs in which a species was detected outside of its native range) of stream fishes in the eastern U.S.A. (Peoples & Midway, 2018). Although certain methods differ between our study and Peoples and Midway's (e.g. definitions of spread and game status, spatial extents), the two studies drew disparate conclusions regarding the ability of non-game versus game species to spread. Whereas we found non-game species more likely to be spreaders in the UMNR, Peoples and Midway (2018, p. 1164) concluded that non-game species "are less likely to colonise many catchments where they are not native because they do not have the traits humans find desirable for fishing". This apparent contradiction may reflect the different spatial grains between the studies. Within a fourth-level HU (particularly in a system lacking lentic habitat), many game species may be restricted to impoundments and mainstem rivers, and therefore do not become as widespread as non-game species regionally adapted to the receiving environment. However, when viewed at a greater spatial grain (i.e. among many fourth-level HUs), game species that have been widely transplanted within a region, even if restricted to a small proportion of the available habitat, can be perceived as being more widespread than non-game species by virtue of their greater total extent.

5 | CONCLUSIONS

We showed that strong colonisers and spreaders share traits that differentiate them from weak colonisers and non-spreaders. However, predictors of invasion success also differed between stages. Residence time, benthic feeding strategy, and parental care (nest spawning) predicted colonisation success, whereas successful spreaders were adapted to warmer winters. Species' geography influenced outcomes of both stages, but the direction of some effects differed between

stages. An equilibrium life-history strategy favoured both colonisation and spread. Other biological traits differed, suggesting a shift in predominant ecological filters between invasion stages. Although propagule pressure did not predict invasion outcomes in any of our models, we found strong links between residence time and colonisation, and between non-game status and the spread of introduced species.

Biological traits predicted colonisation and spread more accurately than ecological traits, and were more directly linked to biological mechanisms. We expect the advantages of models based on biological traits to apply generally across taxa and regions. However, we observed a lack of published data on fundamental biological traits such as egg diameter, larval length, and thermal tolerance for many species. This shortcoming underscores the value of further research on the physiological, morphological, reproductive, and life-history traits of stream fishes.

Our trait-based analyses provided several insights about how prevailing ecological filters shape stream fish assemblages, as well as how those filters may shift in response to anthropogenic changes at landscape scales. Contrary to the hypothesis that abiotic factors are the principal filtering mechanisms determining species' geographic distributions (Peterson et al., 2011; Poff, 1997) and principal determinants of fish invasion success (Moyle & Light, 1996), we found parental care to be an important predictor of invasion success. This finding corroborates other recent studies revealing the importance of biotic factors (Peoples et al., 2017), and nest spawning/association in particular (Hitt & Roberts, 2012; Pendleton, Pritt, Peoples, & Frimpong, 2012; Peoples et al., 2015; Peoples & Frimpong, 2013), in structuring lotic cyprinid assemblages. Nest spawning/association appears to be a principal mechanism mediating the rapid spread of several native invaders in the UMNR. We encourage further studies on the role of spawning-mound builders such as *Nocomis* species in triggering potential invasional meltdowns (Simberloff & Von Holle, 1999) by facilitating invasions by groups of nest associates.

Results of our models for colonisation and spread support the hypothesis that landscape-scale alteration has reconfigured ecological filters in ways that increase the invasibility of UMNR streams. Successful invaders possessed traits commonly hypothesised to enhance performance in warmer, siltier water and conditions of chronic competition/stress. Presumably, restoration practices (e.g. riparian reforestation, livestock exclusion, stormwater retention) aimed at degraded UMNR streams could reduce the success of these invaders.

CONFLICT OF INTEREST

No conflict of interest has been declared by the author(s).

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.