Temporal trends in stream-fish distributions, and species traits as invasiveness drivers in New River (USA) tributaries

by Joseph D. Buckwalter

Thesis submitted to the faculty of the Virginia Polytechnic Institute & State University in partial fulfillment of the requirements for the degree of

Master of Science
in
Fish and Wildlife

Emmanuel A. Frimpong, chair
Paul L. Angermeier
Jacob N. Barney

12 January 2016
Blacksburg, Virginia, United States

Keywords: decline, dispersal, introduced species, nonindigenous species, spread

© Joseph D. Buckwalter, 2016

Temporal trends in stream-fish distributions, and species traits as invasiveness drivers in New River (USA) tributaries

Joseph D. Buckwalter

ABSTRACT

Biological invasions represent both an urgent conservation problem and an opportunity to advance ecological theory. Development of pertinent research questions and proactive management strategies require knowledge of which introduced species are present and of spatiotemporal trends in the distribution of natives and invaders. In Chapter 2 we developed a quantitative framework to identify spreaders and decliners and estimate invasion chronologies based on a historical fish presence data set for upper and middle New River (UMNR) tributaries. Our framework accounts for spatiotemporal variability in sampling effort by aggregating presences by watershed and expressing range size as a function of the number of watersheds sampled per time period. The majority (55%) of fish species present in the study area were introduced, 51% of which were spreaders. Most spreaders (84%) appeared to be spreading exponentially. The rate of new introductions detected in the study area has slowed since the mid-20th century. Two natives, the mound-spawning bluehead chub *Nocomis leptocephalus* and its strong nest associate (reproductive mutualist), mountain redbelly dace *Chrosomus oreas*, were among the most rapid spreaders. Four natives showed evidence of decline. Our framework leverages historical presence data to reconstruct temporal trends in species distributions. It sets the stage for further study of factors driving stream fish invasions and declines in the Appalachian region, and is transferable to diverse taxonomic groups and geographic regions.

Species traits and human activities mediating stream-fish invasions remain poorly understood. In Chapter 3 we modeled the contribution of species traits to invasion success of UMNR tributary fishes during the colonization and spread stages. Biological traits accurately explained colonization and spread success, whereas ecological traits resulted in less accurate models. Colonization success was positively related to time since introduction, benthic feeding, an equilibrium life history, and nest spawning. Successful spread was positively related to winter air temperature in the native range and an equilibrium life history. Variables estimating human use and propagule pressure were non-informative. Traits that influenced invasion success were consistent with the hypothesis that human land-use practices have increased the invasibility of highland watersheds by creating novel conditions suited to lowland and equilibrium invaders.

DEDICATION

"In graduate school I am especially interested in having a rigorous experience in research and improving my academic background and quantitative skills in fisheries science" (from my April, 2012 grad school application cover letter to Emmanuel Frimpong). Thanks to Emmanuel and committee members Paul Angermeier and Jacob Barney, and the tag-team of profs that guided my studies, my wish was granted in full measure. Even more important than the knowledge and quantitative skills, these learned ones stimulated my rusty cognitive circuitry through assignments and discussions consistently ranking high on Bloom's taxonomy. Thinking and creating are arduous, but surrender to ignorance and self doubt marks the start of a long, easy, boring slide into ineptitude. Thanks to your prodding, I got turned around and am aiming for higher ground. Emmanuel was a godsend as an advisor to this erstwhile, wannabe scholar. His patience, wise counsel, and unfailing good humor lifted me through many lows.

I thank my fellow Frimpong labmates and denizens of JCH 113 Brandon Peoples, Caitlin Worsham, Iris Fynn, Jian Huang, Stephen Floyd, Steve Watkins, and Yaw Ansah for befriending this not-so-hip oldster and sharing your wisdom. I especially enjoyed travelling the New River backroads and streambanks in your company. Be courageous in striving to keep this world a fishy place.

This endeavor was made possible, and I was sustained through it by the love, support, and daily sacrifices of my wife Sera and kids Noah, Luke, and Malia. Thank you for inspiring, putting up with, and feeding this computer-hogging grouch over the past three years. And to my parents Robert & Betty Lou, thank you for showing this boy around the good Earth, raising me close to nature, nurturing me in love and the Word, and for encouraging my interests. Finally, I dedicate this thesis to my recently late Grandma Faith who loved all, lived joyfully, served faithfully, and brought out the best in those around her.

ACKNOWLEDGEMENTS

ATTRIBUTION

Three co-authors contributed significantly to this thesis, which is a compilation of two manuscripts. This section specifies the contributions of each co-author to this work. E.A. Frimpong is my academic advisor and primary project supervisor. He wrote the grant to fund this study, and contributed heavily to the project design, analysis and writing of both manuscripts. Paul L. Angermeier and Jacob N. Barney serve on my advisory committee and contributed much to the concepts, study design, and writing of Chapters 2 and 3. This thesis is accordingly written in the first-person plural voice. Some information is redundant between chapters because each chapter was written as a stand-alone manuscript. Chapter 2 is to be submitted for publication to the Journal of Applied Ecology, and Chapter 3 to Diversity and Distributions.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER 1: GENERAL INTRODUCTION

A better understanding of stream-fish invasions is important for managing harmful invasive species, sustaining desirable species and species of concern, and assessing risks and benefits prior to future introductions. Freshwater fishes had the highest extinction rate among vertebrates worldwide in the 20th century, and the modern extinction rate for North American freshwater fishes is conservatively estimated to be 877 times greater than the background rate (Burkhead, 2012). From 1900 to 2010, at least 39 species and 18 subspecies of North American freshwater fishes have gone extinct (Burkhead, 2012), and 39% of described species are imperiled or extinct (Jelks *et al.*, 2008). Through adverse effects such as hybridization, competition, predation, disease, food-web and ecosystem changes, and habitat alteration (Cucherousset & Olden, 2011), invasive species are a leading cause of decline and extinction of North American fishes (Miller, Williams & Williams, 1989; Wilcove *et al.*, 1998; Clavero & García-Berthou, 2005; Light & Marchetti, 2007; Jelks *et al.*, 2008; Burkhead, 2012). The number of newly introduced fish species in inland waters of the USA nearly tripled from the first half to the latter half of the 20th century (Nico & Fuller, 1999). Invasive fish are also implicated in $5.4 billion in annual net economic losses in the USA (Pimentel, Zuniga & Morrison, 2005).

Study of invasions also contributes to an overall understanding of how organisms interact in a changing environment (Vermeij, 1996; Lockwood, Hoopes & Marchetti, 2007). Ecologists regard introduced species as biotic probes or model organisms to test ecological theories such as niche theory and life-history theory (Olden, Poff & Bestgen, 2006), evolutionary responses to novel environments (Sakai *et al.*, 2001; Yonekura, Kawamura & Uchii, 2007) and community responses to environmental change (Olden *et al.*, 2006), and as a measure of anthropogenic disturbance (e.g., Kennard *et al.*, 2005; Vacher, Killingbeck & August, 2007). Cadotte, McMahon & Fukami (2006) discussed the reciprocal relationship between invasion studies and ecological theory. Sax *et al.* (2007) reviewed how invasion studies have contributed to basic research in ecology, evolution, and biogeography, as well as to applied research on extinction, ecosystem function, and response to climate change.

The invasion process is complex, involving multiple interacting biotic and abiotic drivers that often differ between invasion stages (Moyle & Marchetti, 2006). Since the importance of specific invasion drivers often varies with spatial scale and across regions (Kolar & Lodge, 2002; Ruesink, 2005; Moyle & Marchetti, 2006; Lapointe, Thorson & Angermeier, 2012), the drainage

basin is the appropriate basic unit for studies of invasive fishes (Marchetti, Moyle & Levine, 2004b; García-Berthou, 2007).

Invasion terminology and process

Invasion terms have been used in different ways by different authors (Nico & Fuller, 1999; Richardson *et al.*, 2000; Colautti & MacIsaac, 2004; Lockwood *et al.*, 2007; Richardson, Pysek & Carlton, 2011), and there is still no universal usage. For this study, I will use the term "introduced" to describe species not known to occur in the New River drainage prior to European settlement and whose presence is attributable to human actions. I will use the term "native" when referring to species that occurred in the New River drainage prior to European settlement. And I will use the term "invasive" to describe species that have established self-sustaining populations that are spreading into a new environment. Thus invaders may be either introduced or native (e.g., Scott & Helfman, 2001).

Invasion is commonly conceptualized as a staged process (Williamson, 1996; Theoharides & Dukes, 2007; Lockwood *et al.*, 2007), with stages divided by barriers/filters (Richardson *et al.*, 2000; Blackburn *et al.*, 2011) that an introduced species must pass through while expanding beyond its native range and population density. A successful invasion requires a match between the invader and environmental filters of the receiving area. Since alternate suites of filters may be influential as an invasion progresses through its stages (Vermeij, 1996; Marchetti, Moyle & Levine, 2004a; Moyle & Marchetti, 2006), species traits that enhance an invader's fitness may also vary between stages. According to the 'rule of tens' (Williamson, 1996), approximately 10% of introduced species successfully pass through a given invasion stage. However, successful establishment rates are much higher for fishes because they are often introduced intentionally with care taken to ensure a match to the receiving climate and environment (García-Berthou, 2007).

I will adopt Theoharides & Dukes' (2007) four-stage invasion model to conceptualize New River fish invasions. Fig. 1.1 represents the invasion process graphically, showing how filters and invader traits relate to the four invasion stages. The stages are listed below, followed in parentheses by the adjective I will use to describe the status of a species that has passed through the given stage. The most influential types of filters are also listed by stage.

1. Transport (*introduced*): Human-assisted (intentionally or unintentionally) movement and release/escape of fish into the wild in a new location outside of their natural range. Transport filters: Distance and dispersal barriers.

2. Colonization (*casual*): Survival of introduced individuals. Colonization filters: Local abiotic environment.

3. Establishment (*established*): Successful reproduction and the development of self-sustaining populations. Establishment filters: Biotic filters that constrain population dynamics; resource availability; environmental stochasticity.

   A lag phase often occurs between the establishment and spread stages as small populations adapt to the new environment. Lag-phase filters: Population dynamics, isolation of founding colonies, genetic constraints such as inbreeding depression and Allee effects (Sakai et al., 2001).

4. Spread (*invasive*): Dispersal from the source population resulting in the establishment of new populations outside of the area where first introduced. Spread filters: Landscape pattern and connectivity; dispersal barriers; demography; disturbance regime. Based on patterns of spread and abundance, invaders may be further classified as widespread (but rare), localized (but abundant), or widespread and abundant (Colautti & MacIsaac, 2004).

Invasion drivers

Various factors (drivers) such as abiotic and biotic filters, invader traits, and human activities influence the invasion process (Fig. 1.1). Drake *et al.* (1989) described two broad classes of invasion drivers: invasiveness drivers (invader traits) and invasibility drivers (susceptibility of receiving environment). This dichotomy forms the core of subsequent conceptual frameworks of invasion drivers (e.g., Barney & Whitlow, 2008; Catford, Jansson & Nilsson, 2009; Foxcroft, Pickett & Cadenasso, 2011). However, propagule pressure (number of individuals released combined with number of release events) (Lockwood, Cassey & Blackburn, 2005) and various other human influences (e.g., dispersal barriers, land use) are also recognized as important factors. Furthermore, stream-fish invasions, like other ecological processes shaping riverine communities, are probably best explained by a combination of local- and regional-scale factors that vary spatially and temporally across dendritic stream networks (Poff, 1997; Angermeier & Winston, 1998; García-Berthou, 2007; Brown *et al.*, 2011). Thus, the context in

which the invasion unfolds must be considered in concert with mechanisms of invasiveness and invasibility.

Peterson *et al.*'s (2011) Biotic-Abioitic-Movement (BAM) diagram provides a conceptual framework integrating three broad sets of invasion drivers. The BAM diagram represents areas (geographic space) where biotic interactions with other species are favorable (B), abiotic conditions and resources are suitable (A), and that are accessible (M). B∩A∩M defines occupied areas (O). B∩A∩M^c defines invadable areas (I). A modified BAM diagram (BAM-H, Fig. 1.2) emphasizes that humans (H) have altered drivers of B, A, and M (and therefore O and I also) (Catford *et al.*, 2009). A is related to Hutchinson's (1957) concept of the fundamental niche, and A∩B is related to the realized niche. I will apply these conceptual frameworks to understand fish invasions in the New River drainage.

Study area

The New River drains 21,700 km^2 of the Appalachian Mountains in North Carolina (NC), Virginia (VA), and West Virginia (WV). In this study I focused on tributaries of the 9,700 km^2 upper and middle portion of the New River drainage (UMNR) in NC and VA (Fig. 2.1). I excluded the mainstem New River due to insufficient fish community sampling (most collections targeted game species). I excluded the WV portion because comprehensive fish collection records in an electronic format were unavailable. The UMNR lies in two physiographic provinces: the Blue Ridge, and Valley and Ridge (Jenkins & Burkhead, 1994). Underlying geology in the UMNR is primarily igneous in the Blue Ridge and sedimentary (carbonate and shale) in the Valley and Ridge. From its montane headwaters in the Blue Ridge highlands near Boone, NC, the New River flows north into VA, crosses the rolling, agricultural New River plateau, then heads northwest, cutting across the long, parallel ridges of the Valley and Ridge before dropping into the New River Gorge in WV. Kanawha Falls in WV marks the downstream end of the New River, 560 river km from its source. Below Kanawha Falls it is known as the Kanawha River, which flows to the Ohio River. Major UMNR tributaries include the North and South forks in NC, and Reed, Big Reed Island, Walker, and Wolf creeks and Little River in VA.

The New River drainage provides an ideal natural laboratory in which to study BAM-H influences on native and introduced fishes. With the highest proportion of introduced species of any eastern USA drainage, the New River provides a diverse set of invasion scenarios for study.

Secondly, the New River drainage has a disproportionately large number of endemic species (9) relative to its native species richness (44) (Jenkins & Burkhead, 1994). Endemism of the receiving area has been linked to invasion success (Ruesink, 2005), and also provides impetus from a conservation standpoint to investigate invasion impacts on endemics. Thirdly, the New River drains three distinct physiographic provinces (Blue Ridge, Ridge and Valley, and Allegheny Plateau), which provide alternate abiotic contexts in which to investigate invasion outcomes. Finally, watersheds of the New River drainage span spatial and temporal gradients of human land-use practices such as deforestation, agriculture, strip mining, and urbanization. Land cover in the study area comprises 63% forest, 28% agricultural, and 7% developed lands (Fry *et al.*, 2011; Fig. 2.1). Six hydroelectric dams on 4th+ order streams were completed from 1902 to 1939 (Fig. 2.1), which, along with hundreds of smaller dams and farm ponds, have been persistently stocked with introduced game and forage fish. These activities have created novel conditions (e.g., increased water temperature, siltation and nutrients; reduced dissolved oxygen, water clarity and velocity) preferred (or tolerated) by some species, but less suitable to others, particularly native highland specialists adapted to clear, cool water (Angermeier & Winston, 1998; Jones *et al.*, 1999; Scott & Helfman, 2001; Hitt & Roberts, 2012; Lapointe *et al.*, 2012).

Goal and objectives

My goal was to reconstruct the spread and decline of UMNR stream fishes and explore species traits driving invasions. I pursued two objectives to meet this goal: 1. Compile a historical UMNR fish-collection data set and classify spreaders and decliners; 2. Examine species traits contributing to the spread and decline of stream fishes in the UMNR.

References

Angermeier P.L. & Winston M.R. (1998) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**, 911–927.
Barney J.N. & Whitlow T.H. (2008) A unifying framework for biological invasions: the state factor model. *Biological Invasions*, **10**, 259–272.
Blackburn T.M., Pysek P., Bacher S., Carlton J.T., Duncan R.P., Jarosik V. *et al.* (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, **26**, 333–339.
Brown B.L., Swan C.M., Auerbach D.A., Campbell Grant E.H., Hitt N.P., Maloney K.O. *et al.* (2011) Metacommunity theory as a multispecies, multiscale framework for studying the

influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society*, **30**, 310–327.

Burkhead N.M. (2012) Extinction rates in North American freshwater fishes, 1900–2010. *BioScience*, **62**, 798–808.

Cadotte M.W., McMahon S.M. & Fukami T. (2006) *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature*. Springer, Dortrecht, The Netherlands.

Catford J.A., Jansson R. & Nilsson C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions,* **15**, 22–40.

Clavero M. & García-Berthou E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, **20**, 110.

Colautti R.I. & MacIsaac H.J. (2004) A neutral terminology to define 'invasive' species. *Biodiversity Research*, **10**, 135–141.

Cucherousset J. & Olden J.D. (2011) Ecological impacts of non-native freshwater fishes. *Fisheries*, **36**, 215–230.

Drake J.A., Mooney H.A., Di Castri F., Groves F., Kruger F.J., Rejmanek M. *et al*. (1989) *Biological Invasions: a Global Perspective*. John Wiley and Sons, New York.

Foxcroft L.C., Pickett S.T.A. & Cadenasso M.L. (2011) Expanding the conceptual frameworks of plant invasion ecology. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 89–100.

Fry J., Xian G., Jin S., Dewitz J., Homer C., Yang L. *et al.* (2011) Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing*, **77**, 858-864.

García-Berthou E. (2007) The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology*, **71** (Supplement D), 33–55.

Hitt N.P. & Roberts J.H. (2012) Hierarchical spatial structure of stream fish colonization and extinction. *Oikos*, **121**, 127-137.

Hutchinson G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Jelks H.L., Walsh S.J., Burkhead N.M., Contreras-Balderas S., Diaz-Pardo E., Hendrickson D.A. *et al.* (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, **33**, 372–407.

Jones E.B.D. III, Helfman G.S., Harper J.O. & Bolstad P.V. (1999) Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology*, **13**, 1454–1465.

Kennard M.J., Arthington A.H., Pusey B.J. & Harch B.D. (2005) Are alien fish a reliable indicator of river health? *Freshwater Biology*, **50**, 174-193.

Kolar C.S. & Lodge D.M. (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science*, **5596**, 1233–1235.

Lapointe N.W.R, Thorson J.T. & Angermeier P.L. (2012) Relative roles of natural and anthropogenic drivers of watershed invasibility in riverine ecosystems. *Biological Invasions*, **14**, 1931–1945.

Light T. & Marchetti M.P. (2007) Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology*, **21**, 434–446.

Lockwood J.L., Cassey P. & Blackburn T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

Lockwood J.L., Hoopes M.F. & Marchetti M.P. (2007) *Invasion Ecology*, 2nd edition. Blackwell Publishing, Oxford, UK.

Marchetti M.P., Moyle P.B. & Levine R. (2004a). Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology*, **49**, 646-661.

Marchetti M.P., Moyle P.B. & Levine R. (2004b) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications*, **14**, 587–596.

Miller R.R., Williams J.D. & Williams J.E. (1989) Extinctions of North American fishes during the past century. *Fisheries*, **14**, 22–38.

Moyle P.B. & Marchetti M.P. (2006) Predicting invasion success: freshwater fishes in California as a model. *BioScience*, **56**, 515–524.

Nico L.G. & Fuller P.L. (1999) Spatial and temporal patterns of nonindigenous fish introductions in the United States. *Fisheries*, **24**, 16–27.

Olden J.D., Poff N.L. & Bestgen K.R. (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs*, **76**, 25–40.

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M. *et al.* (2011) Niches and geographic distributions. Chapter 3 In: *Ecological Niches and Geographic Distributions. Monographs in Population Biology*, **49**. Princeton University Press, Princeton, New Jersey.

Pimentel D., Zuniga R. & Morrison D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.

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

Richardson D.M., Pysek P. & Carlton J.T. (2011) A compendium of essential concepts and terminology in invasion ecology. Chapter 30 In: Richardson D.M., editor. *Fifty Years of Invasion Ecology: the Legacy of Charles Elton*, 1st edition. Blackwell Publishing, Oxford, UK.

Richardson D.M., Pysek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Ruesink J.L. (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology*, **19**, 1883–1893.

Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A. *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology, Evolution, and Systematics*, **32**, 305–332.

Sax D.F., Stachowicz J.J., Brown J.H., Bruno J.F., Dawson M.N., Gaines S.D. *et al.* (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution*, **22**, 465–471.

Scott M.C. & Helfman G.S. (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, **26**, 6–15.

Theoharides K.A. & Dukes J.S. (2007) Plant invasions across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256–273.

Vacher K.A., Killingbeck K.T. & August P.V. (2007) Is the relative abundance of nonnative species an integrated measure of anthropogenic disturbance? *Landscape Ecology*, **22**, 821–835.

Vermeij G.J. (1996) An agenda for invasion biology. *Biological Conservation*, **78**, 3–9.

Wilcove D.S., Rothstein D., Dubow J., Phillips A. & Losos E. (1998) Threats to imperiled species in the United States. *BioScience*, **48**, 607–615.

Williamson M. (1996) *Biological Invasions*. Chapman & Hall, London.

Yonekura R., Kawamura K. & Uchii K. (2007) A peculiar relationship between genetic diversity and adaptability in invasive exotic species: bluegill sunfish as a model species. *Ecological Research*, **22**, 911–919.
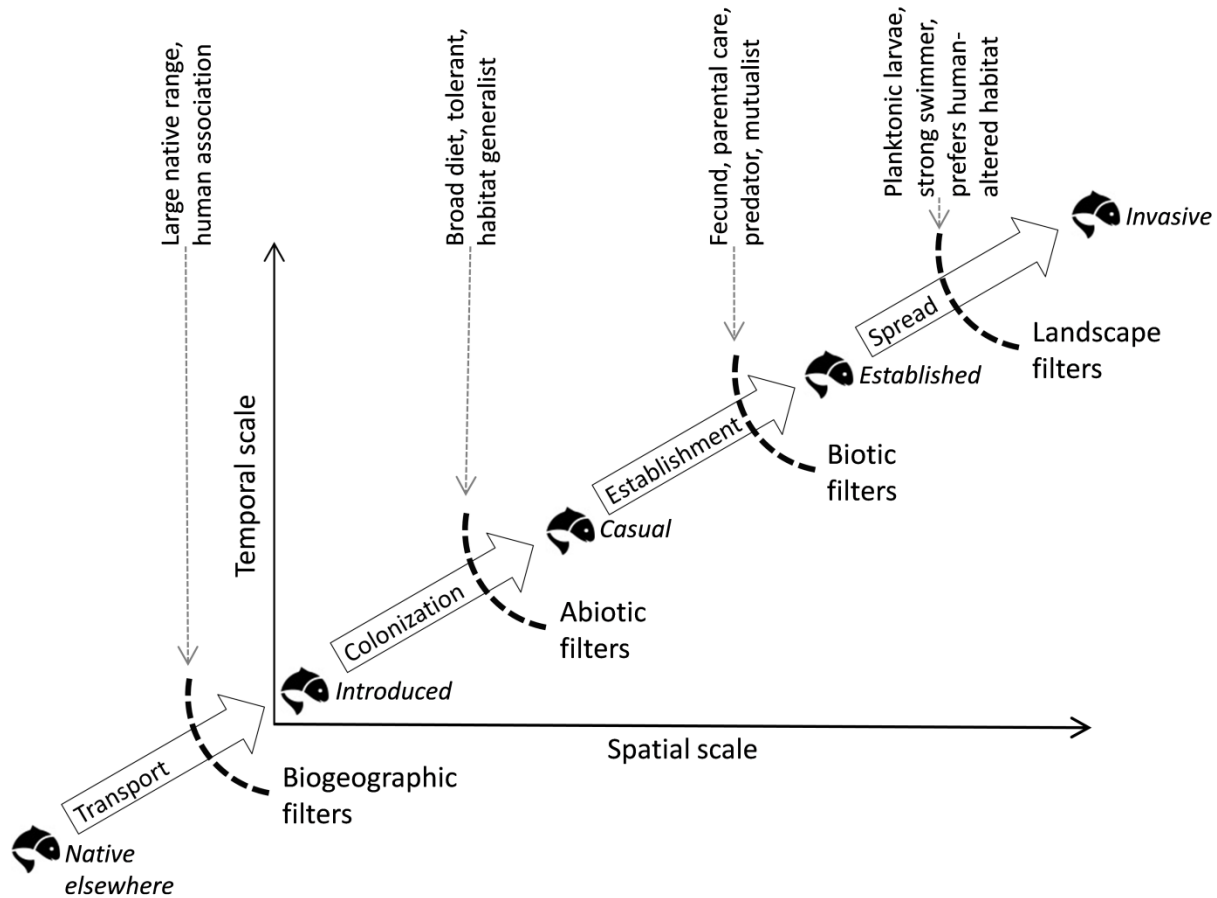
Fig. 1.1 Four-stage invasion model adapted from Theoharides & Dukes (2007). A would-be invader must possess traits (example traits labeled along top of figure) enabling it to surmount the suite of filters/ barriers characteristic of each stage. As an invasion progresses through the stages, the temporal and spatial extents of invasion processes generally increase. The transport stage is shown outside the spatial and temporal axes because human-assisted transplants of introduced species can occur much faster, and over larger distances, than most natural movements of species.
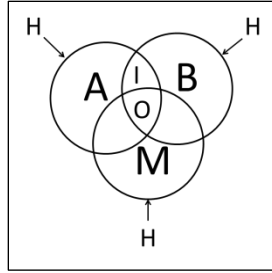
Fig. 1.2 The **B**iotic-**A**biotic-**M**ovement-**H**uman (BAM-H) diagram adapted from Peterson *et al.* (2011) and Catford *et al.* (2009) represents distributional areas for a given species, including areas where biotic interactions with other species are favorable (B), abiotic conditions and resources are suitable (A), and that are accessible (M). B∩A∩M defines occupied areas (O). B∩A∩M^c defines invadable areas (I). Humans (H) may modify B, A, or M (and therefore O and I also).

CHAPTER 2: HISTORICAL PRESENCE DATA REVEAL SUCCESSFUL STREAM-FISH INVADERS AND DECLINING NATIVES IN AN APPALACHIAN (USA) DRAINAGE BASIN

Running title: New River spreaders and decliners

Keywords: dispersal, freshwater, invasion rate, lotic, nest association, population growth, range expansion, species distribution, spread, time-series

Summary

1. Biological invasions represent both an urgent conservation problem and an opportunity to advance ecological theory. Development of pertinent research questions and proactive management strategies require knowledge of which introduced species are present and of spatiotemporal trends in the distribution of natives and invaders.

2. We developed a quantitative framework to identify spreaders and decliners and estimate invasion chronologies based on a historical fish presence data set for an Appalachian (USA) drainage basin. Our framework accounts for spatiotemporal variability in sampling effort by aggregating presences by watershed and expressing range size as a function of the number of watersheds sampled per time period.

3. The majority (55%) of fish species present in the study area were introduced, 51% of which were spreaders. Most spreaders (84%) appeared to be spreading exponentially. The rate of new introductions detected in the study area has slowed since the mid-20th century.

4. Two natives, the mound-spawning bluehead chub *Nocomis leptocephalus* and its strong nest associate (reproductive mutualist), mountain redbelly dace *Chrosomus oreas*, were among the most rapid spreaders. Four natives showed evidence of decline.

5. Our framework leverages historical presence data to reconstruct temporal trends in species distributions. It sets the stage for further study of factors driving stream fish invasions and declines in the Appalachian region, and is transferable to diverse taxonomic groups and geographic regions.

Introduction

Biological invasions occur when introduced species spread and become abundant in new areas (Richardson *et al.*, 2000; Rejmánek *et al.*, 2002). The number of newly introduced fish species in USA inland waters nearly tripled from the first to the latter half of the 20th century (Nico & Fuller, 1999). Through adverse effects such as hybridization, competition, predation, disease, food-web and ecosystem changes, and habitat alteration (Cucherousset & Olden, 2011), invasions are among the leading causes of extinction of freshwater fishes globally (Helfman, 2007). In North America, where 39% of freshwater fishes are imperiled or extinct (Jelks *et al.*, 2008), invasions were cited as a detrimental factor in 68% of freshwater fish extinctions (Miller, Williams & Williams, 1989; Clavero & García-Berthou, 2005). Fish invasions are also

expensive, causing an estimated $5.4 billion in annual net economic losses in the USA (Pimentel, Zuniga & Morrison, 2005).

Understanding invasions and the factors that contribute to their success is of practical and conceptual importance. Practical considerations include early detection of invaders, identifying their adverse effects, prioritizing management actions, indicating the health of water bodies (Scott & Helfman, 2001; Kennard *et al.*, 2005; Vacher, Killingbeck & August, 2007), and assessing risks and benefits of future introductions. Conceptually, invasions serve as natural experiments to test ecological and evolutionary theories (Vermeij, 1996; Sakai *et al.*, 2001; Olden, Poff & Bestgen, 2006; Yonekura, Kawamura & Uchii, 2007). Since the importance of specific invasion drivers varies regionally (Kolar & Lodge, 2002; Ruesink, 2005; Moyle & Marchetti, 2006), the drainage basin is the appropriate basic unit for studies of invasive fishes (Marchetti, Moyle & Levine, 2004; García-Berthou, 2007). However, our ability to ask the right questions and prioritize and develop relevant and effective interventions and preventative treatments is predicated on basic knowledge of which introduced species are present, and of spatiotemporal trends in the distribution of native and non-native species.

The New River has the highest proportion of introduced to native fishes of any eastern USA drainage and the second highest proportion of endemic fishes (Jenkins & Burkhead, 1994), yet no prior quantitative studies of fish invasions were identified. Our objective for this study was to develop a framework for leveraging historical presence data to reconstruct temporal trends in species distribution using New River stream fishes as a model system. This framework set the stage for exploration of spatiotemporal patterns of spread and decline among introduced and native species.

Idealized population growth, including that of spreading invaders, is expected to follow a logistic pattern (Fig. 2.2) (Quinn & Deriso, 1999; Lockwood, Hoopes & Marchetti, 2007). After the initial latent (lag) phase, range size increases exponentially to a maximum rate of spread (inflection point of logistic growth curve). During the subsequent stable phase the invasion rate becomes increasingly dampened as the invadeable area approaches saturation. However, depending on the introduction chronology and historical sampling regime, the window of time captured in a time-series dataset of species distribution records may cover only a portion of the logistic curve, during which the invasion rate may exhibit a stable (not increasing or decreasing), or exponentially or linearly increasing form (e.g., areas A–E in Fig. 2.2). By modeling the form

13

of spread observed for a number of invasions in a region we can explore temporal trends in regional invasion rates and potentially identify introduced species likely to continue spreading, while enabling future studies to probe biological, environmental, and contextual factors that drive invasions.

The logistic population growth curve is subject to modification by alterations to the abiotic or biotic environment. However, except where the environment has been greatly altered from its natural state, native species as a group, given their longer evolutionary history in a basin, likely maintain a state of relative equilibrium in spatial distribution (stable phase), while successfully established introduced species continue to spread until suitable areas are filled. Thus, examining relative rates of spread for introduced versus native species may provide insight into the degree to which introduced species have achieved equilibrium. Furthermore, by comparing the rates of spread for the subset of native and introduced species whose initial range sizes (i.e., at the start of the time period during which spread rates are being compared) overlap, the question of whether introduced species are inherently (e.g., as a result of their invasive traits) more capable of spreading than natives can be explored.

Based on the premise of logistic spread, and given a spatially and temporally referenced species distribution dataset for a pool of established invaders having a range of invasion chronologies, we hypothesized that invaders will exhibit distinct forms of spread (exponential, linear, logistic, or none [stable]) depending on which invasion phases are captured in the time frame of observations. We expected that the following three explanatory variables describing invasion histories would explain much of the variation in the form of spread observed among invaders:

1. Generations since first detected *GensSinceDetect* (surrogate for generations since introduction). The stage of invasion, and therefore the observed form of spread, is dependent on time since introduction (Barney & Whitlow, 2008; Catford, Jansson & Nilsson, 2009). However, due to the strong negative relationship between population growth and generation time (Winemiller & Rose, 1992), *GensSinceDetect* may be a more efficient predictor of the form of spread than time measured in years.

   - **Hypothesis 1** With increasing *GensSinceDetect*, form of spread will progress from stable/linear (lag phase) to exponential (exponential phase) and eventually back to stable/linear (stable phase). Species for which the time-series distribution data span at

14

least the exponential and stable phases will exhibit an overall logistic form. Species sampled during the rising limb (spanning the inflection point) of the exponential phase may exhibit a linear form, but with a relatively high rate of spread.

2. Initial catch per unit effort *CPUE1* (range size at time zero).The CPUE (e.g., proportion of units sampled where the focal species was present) is preferred to raw presence data because CPUE accounts for temporal variation in sampling effort.

   - **Hypothesis 2** *CPUE1* will help differentiate species exhibiting a stable or linear form of spread that are still in lag phase (i.e., recent introductions) from earlier introductions that may have reached the stable phase prior to time zero in the dataset.

3. Propagule pressure *IntroEffort* (estimated number of individuals transplanted into the receiving environment). *IntroEffort* influences establishment success and invasion rates (Lockwood, Cassey & Blackburn, 2005). *IntroEffort* records may be available for certain species, or can be estimated based on expert knowledge (e.g., Marchetti *et al.*, 2004).

   - **Hypothesis 3** Species having higher *IntroEffort* will exhibit relatively high rates of spread and/or a shortened lag phase (i.e., fewer *GensSinceDetect* prior to exponential growth).

Methods

Study area and fauna

This study was conducted in tributaries of the upper and middle portion of the New River drainage of North Carolina and Virginia, USA, hereafter referred to as the UMNR (Fig. 2.1). Located in the central Appalachian Mountains, the UMNR drains approximately 10,000 km^2 of two major ecoregions: the Blue Ridge, and Valley and Ridge (Omernik, 1987). Underlying geology is primarily igneous in the Blue Ridge and sedimentary (carbonates and shale) in the Valley and Ridge. The upper and middle New River subbasins have the highest average elevation (829 m and 764 m, respectively) of Virginia's 39 subbasins (J. Buckwalter, unpubl. data).

Land cover in the UMNR comprises 63% forest, 28% agricultural, and 7% developed lands (Fry *et al.*, 2011; Fig. 2.1). A series of five hydroelectric dams on the New River mainstem and one on the largest UMNR tributary, Little River (Virginia), ranging in height from 4 to 42 m

were constructed from 1902 to 1939 (Fig. 2.1). The largest, Claytor Dam, impounds a 34-km-long, 1819-ha mainstem reservoir (Rosebery, 1951), which, along with hundreds of smaller hydroelectric, recreation, flood-control and farm impoundments in the UMNR, have been repeatedly stocked with non-native game and prey fishes over the past century (Jenkins & Burkhead, 1994).

Although the New River drainage, with just 44 native fish species, is considered the most depauperate of all 26 major eastern USA drainages, it has a disproportionately large number of both endemic (9) and introduced (55) species. The New River's depauperacy and high rate of endemism are due in large part to a barrier falls at the outlet and the montane aspect of the drainage (Jenkins & Burkhead, 1994). The depauperate New River fauna included few native gamefish species. However, state-sanctioned stocking of non-native game and prey species from the mid-19th century through the 1970s, supplemented by unauthorized inter-basin transfers of baitfish since the mid-20th century, have added 55 established introduced fish species, such that the New River has the greatest proportion of introduced-to-native species (55:44) among eastern USA drainages (Jenkins & Burkhead, 1994; New River figures updated in this study). The greater Kanawha hydrologic subregion containing the New River drainage had more introduced fishes (65) than any other subregion in the USA (Nico & Fuller, 1999).

Several UMNR characteristics mentioned above make this a particularly suitable system in which to study stream-fish invasions: (1) Since approximately half of its extant fishes were introduced, the UMNR offers a sufficient number of invasion cases for statistical analyses; (2) While no community is immune to invasion, depauperate ecosystems such as the UMNR are hypothesized to be more susceptible to major community impacts such as decline and extirpation of native species (Moyle & Light, 1996); (3) Endemism of the receiving area has been linked to invasion success (Ruesink, 2005), and also provides impetus from a conservation standpoint to investigate invasion impacts on endemics; (4) The UMNR's two ecoregions provide alternate abiotic contexts in which to investigate invasion outcomes; (5) UMNR watersheds span spatial and temporal gradients of human land-use practices that provide opportunities to observe human influences on invasion processes. For instance, deforestation, agriculture, strip mining, urbanization, and impoundment have transformed many Appalachian highland streams functionally into lower-elevation streams by increasing water temperature, fine sediment and nutrient inputs, and availability of lentic habitats (Jones *et al.*, 1999). These novel conditions

often favor lowland generalist native and non-native species, but are less suitable to native highland specialists (Angermeier & Winston, 1998; Jones *et al.*, 1999; Scott & Helfman, 2001; Hitt & Roberts, 2012; Lapointe *et al.*, 2012).

Fish-collection data sources

Introduced fishes have become widespread throughout river networks in as little as five (Jennings, 1988; Wikramanayake, 1990) or ten (Neely & George, 2006), to over 20 years (Walters *et al.*, 2008); therefore, a database spanning decades was needed to reconstruct invasion histories for multiple species. Since such a data set did not exist, we compiled spatially and temporally referenced fish-collection records for the UMNR.

The VA Department of Game & Inland Fisheries' (VDGIF) Fish & Wildlife Information Service (VAFWIS, 2013) was the most comprehensive source available of fish-collection data for VA. The VAFWIS serves as an online clearing house for VDGIF's biological databases and includes records compiled from scientific collections and literature reviews.

Menhinick (1991) provided the most comprehensive source of historical fish distribution records for the NC portion of the UMNR. The full NC dataset used by Menhinick (1991) was not available electronically; however, according to W.C. Starnes (NC Museum of Natural Sciences [NCSM], Raleigh, personal communication), Menhinick's two main sources for the New River drainage—NCSM collection records, and Richardson & Carnes (1964) (whose voucher specimens were confirmed and records georeferenced by Starnes & Hogue, 2011)—have since been made available by the NCSM (2014), along with additional records not available to Menhinick. Additional recent (e.g., 1990s to present) fish-collection data for NC were provided by SFCAP (2014).

Several other sources provided additional UMNR fish-collection records, including: (1) The Multistate Aquatic Resources Information System (MARIS, 2013), which contained recent (1990s–2013) fish-community records from VA (data originator: VA Department of Environmental Quality); (2) FishNet2 (2014), an online data portal of fish specimen data from institutions around the world, including over 30 in the USA; (3) The U.S. Environmental Protection Agency (USEPA, 2013), which sampled New River fish communities in NC and VA during the 1990s; and (4) the authors' recent collections, described below.

Contemporary UMNR fish sampling

In addition to compiling historical fish collection data (described above), we conducted our own fish-community sampling in wadeable streams at a total of 120 UMNR sites during the summers of 2008–2009 and 2012–2014. Sites were selected to represent a spatially balanced sample of UMNR watersheds and a range of catchment land-use types and levels. In 2008–2009, we used 2-shocker, 3-pass backpack electrofishing in one reach of 20–30 mean channel widths in length per site (Peoples, Tainer & Frimpong, 2011). In 2012–2014 we used 2-shocker, 1-pass backpack electrofishing in two spatially replicated reaches of 80–100 m in length located within the same inter-confluence stream segment and each reach encompassing at least two pool-riffle sequences. Data from both reaches were combined to represent a single site for this study. Sixty of 80 sites sampled in 2012–2014 were repeat-sampled at least one more season during the three-year period.

Data compilation

We compiled all UMNR fish collection records into a single data set including latitude and longitude, collection year, scientific name, and sixth-level hydrologic unit code (HUC12). The USA Watershed Boundary Dataset (WBD) (Simley & Carswell, 2009) represents watershed boundaries nested within six hierarchical levels. Sixth-level units are known as subwatersheds or HUC12s (because they are uniquely identified by a 12-digit code). The UMNR comprised 100 HUC12s averaging 95 km^2. We aggregated records such that each species was listed only once per HUC12 and year. Since few whole-community collections were reported from the mainstem New River (most sampling in the mainstem has exclusively targeted game species), we excluded all mainstem collections from the data set. We deleted records of species whose occurrence in the New River drainage is unconfirmed, including *Chrosomus tennesseensis*, *Nocomis micropogon, N. raneyi, Luxilus cornutus, Cottus baileyi,* and *Percina maculata*. These species were likely either misidentified or entered mistakenly (M. Pinder, VDGIF, Blacksburg, personal communication). Records for another 18 species reported from only one HUC12 and only one year were removed. Because our focus was on stream fishes, we also excluded six species typically restricted to the mainstem or large reservoirs in the UMNR (*Alosa pseudoharengus, Esox masquinongy, Pylodictis olivaris, Morone saxatilis, M. chrysops, Sander vitreus*). The final

77-year data set (1938–2014) contained 19,424 unique records from 2,332 UMNR collection events.

Finally, we partitioned the data set into ten time periods: period 1 = 1938–1953; period 2 = 1954–1962; period 3 = 1963–1969; period 4 = 1970–1976; period 5 = 1977–1983; period 6 = 1984–1996; period 7 = 1997–1998; period 8 = 1999–2007; period 9 = 2008–2011; period 10 = 2012–2014. Time periods were set to allocate the 2,332 collections approximately evenly among the ten time periods (~10% or 233 collection per time period), while maintaining a minimum sampling intensity (proportion of HUC12s sampled) of 50% in each time period. We also created a series of maps showing the spatial distribution of UMNR fish-collection sites to visually assess the spatial evenness of sampling in each time period. Of the 100 UMNR HUC12s, $N_1 = 56$ HUC12s had collections in period 1, $N_2 = 58$ in period 2, $N_3 = 54$ in period 3, $N_4 = 56$ in period 4, $N_5 = 65$ in period 5, $N_6 = 64$ in period 6, $N_7 = 70$ in period 7, $N_8 = 68$ in period 8, $N_9 = 71$ in period 9, and $N_{10} = 64$ in period 10.

Although we treated the fish-collection data as presence-only (information on species absence was not required for our analysis), temporal unevenness of false absences (i.e., non-detection of a resident species) could bias the time series for a given species. By aggregating collections by HUC12, we reduced the prevalence of false absences. To screen for major differences in fish-sampling effort between time periods, which could give rise to unevenness of false absences, we made box plots of the log (x) transformed number of fish collections per HUC12 by time period and the log ($x+1$) transformed number of non-game species reported per collection by time period. The number of non-game species indicates the extent to which the whole fish assemblage (e.g., not just a few select game species) was sampled. If the distribution of collections per HUC12 and non-game species per collection remains stable across time periods, the false-absence rate is likewise expected to remain relatively constant. Game species included *Amia calva*, esocidae, ictaluridae (except for *Noturus* spp.), salmonidae, moronidae, centrarchidae, *Sander vitreus*, and *Perca flavescens*. All other species were considered to be non-game.

Classifying spreaders, decliners, and stable species

We developed a hierarchical framework to classify UMNR stream fishes based on temporal trends in species distribution. First, to account for the unequal number of HUC12s

sampled each time period, we defined catch per unit effort (CPUE) for each species by time period as:

$$CPUE_i = n_i/N_i \tag{1}$$

where: n_i = the number of HUC12s the given species was detected in during time period i; and N_i = the total number of HUC12s sampled during time period i. We then regressed CPUE (y) against a continuous time vector $x = \{15, 24, 31, 38, 45, 58, 60, 69, 73, 76\}$ representing the number of years from 1938 (year 0 in our data set) to the end of each time period, calculated as:

$$x_i = t_i - 1938 \tag{2}$$

where: t_i = the last year in time period i.

   To improve our ability to detect various possible patterns in the CPUE time series, and to explore hypotheses about forms of spread, we fit the following six curves to the (up to) ten (x, y) data points for each species. These curves, hereafter referred to as "models", represent a null hypothesis (no trend in CPUE) and five alternative hypotheses describing possible forms of spread (or decline):

Intercept-only (null) model:	$y = \beta_0$	(3)
Linear model:	$y = \beta_0 + \beta_1 x$	(4)
2-parameter exponential model: (asymptote at $y = 0$)	$y = \beta_0 e^{\beta_1 x}$	(5)
3-parameter exponential model: (horizontal asymptote a estimated)	$y = a + \beta_0 e^{\beta_1 x}$	(6)
3-parameter logistic model: (lower asymptote at $y = 0$, upper asymptote b estimated)	$y = \dfrac{b}{1 + e^{-\beta_1(x - x_{mid})}}$	(7)
4-parameter logistic model: (lower & upper asymptotes estimated)	$y = a + \dfrac{b - a}{1 + e^{(x_{mid} - x)/\beta_1}}$	(8)

where: β_0 = y-intercept or scale; β_1 = slope or growth rate, x_{mid} = inflection point, and a & b = lower and upper asymptotes.

   We defined a *Distribution trend* response variable having four ordinal classes: strong spreader; weak spreader; stable; and decliner. *Distribution trend* and the best model of spread/decline were determined for each species based on the following hierarchical decision framework (Fig. 2.3): (1) Compute Akaike's Information Criterion (Akaike, 1973) corrected for

small samples (AICc) (Hurvich & Tsai, 1989) and Akaike weights for each of the six fitted models, by species. Akaike weights (w_i) sum to 1 and indicate the probability that model i is the best of the candidate models (Burnham & Anderson, 2002). (2) Use w_i for the null model to determine whether there was any trend in the CPUE time series. We classified as *stable* (no trend in CPUE) all species for which the null model had $w_i \geq 0.50$, and the rest as *changing*. An Akaike weight ≥ 0.50 for the null model indicates that the null model is more plausible than all the competing models combined. (3) For the *changing* species we selected the best of the five competing models based on AICc—The best model had the lowest AICc. (4) The *changing* species were further split based on regression coefficients estimated for the five competing models. Species having a negative β_1 upper 90% confidence limit (UCL) for any model were classified as *decliners*. Species having a positive β_1 lower 90% confidence limit (LCL) for any model were classified as *spreaders*. Any remaining species having neither a negative β_1 UCL nor a positive β_1 LCL were added to the stable group. (5) Spreaders having β_1 for the linear model $\geq$ 0.0040 (equivalent to a range increase of at least one HUC12 every 2.5 years) were further classified as *strong spreaders*, and those having $\beta_1 < 0.0040$ as *weak spreaders*. (6) Finally, we screened the stable group for species that would otherwise qualify as spreaders or decliners in Step 4 based on β_1 confidence limits and considered moving them from the stable group to spreaders or decliners based on $\text{AICc}_i - \text{AICc}_{min}$ (Δ_i). Competing models within 2 AICc units of the best model ($\Delta_i \leq 2$) are substantially supported by the data, while models having $2 < \Delta_i \leq 7$ have some support (Burnham & Anderson, 2002).

We chose β_1 of the linear model as the basis to classify strong versus weak spreaders because it represents the average rate of change in CPUE across the study period. We set $\beta_1 = 0.0040$ as the threshold separating strong and weak spreaders because there was a natural break in the distribution of β_1 for UMNR spreaders at 0.0040. In classifying spreaders and decliners, α was relaxed to 0.1 because of the small sample size (5–10 time periods) in the regressions. To help visualize spatio-temporal patterns of spread and decline, we mapped presences of strong spreaders and decliners by time period.

We used R statistical software (R Core Team, 2014) for all analyses. The *lm* function was used to fit the null and linear models, and the *nlsLM* function in the minpack.lm package (Elzhov *et al.*, 2013) was used to fit the exponential and logistic models. β_1 confidence limits were computed with the *confint* function, which uses a direct formula based on t values for linear

models, and the profile-likelihood method for nonlinear models. The *AICc* function in the AICcmodavg package (Mazerolle, 2015) was used to compute AICc values.

Comparing spread rates of introduced and native species

To test whether introduced species are currently spreading at a faster rate than natives, we regressed average rate of spread ($100 \times \beta_1$ of the linear model, units = HUC12s/year) against initial range size (first non-zero CPUE, *iCPUE*) and tested for equality of slopes for introduced versus native species. To explore whether introduced species are inherently more capable of spreading than natives, we repeated the regression, excluding species from either group whose *iCPUE* fell above or below the range observed for species in the other group.

Modeling form of spread for introduced species

We performed classification tree analysis (De'ath & Fabricius, 2000) of the form of spread exhibited during the 77-year study period by the 39 introduced UMNR tributary species. The response variable *Form* had four nominal classes. Species classified as *Distribution trend* = stable were assigned *Form* = Sta. Species classified as spreaders were assigned *Form* = Exp, Lin, or Log based on which competing model gave the lowest AICc in the regressions of CPUE against time. The three explanatory variables hypothesized to influence *Form* were initial CPUE (*CPUE1*), propagule pressure (*IntroEffort*), and generations since first detected (*GensSinceDetect*). We defined *CPUE1* as the CPUE at the end of time-period 1 (numeric, with possible values ranging from 0 to 1). *IntroEffort* was a 3-class ordinal variable scored by regional experts on introduced stream fishes from NC (B. Tracy, NC Department of Environmental Quality [NCDEQ], Raleigh) and VA (M. Pinder, VDGIF, Blacksburg): 1 = an estimated total of <100 individuals were released to the UMNR since European settlement; 2 = 100–1000 individuals released; 3 = more than 1000 individuals released. *GensSinceDetect* was calculated as *t/GenTime,* where $t =$ 2014 minus the year each species was first detected in the New River drainage (Table S1), and *GenTime* = the average age of parents at the time their young are born. We estimated *GenTime* according to equations given by Froese & Binohlan (2000) based on maximum length, length at maturity, and age at maturity data from Jenkins & Burkhead (1994). Maximum length was based on specimens from Virginia or neighboring states reported by

22

Jenkins & Burkhead (1994) or the authors' contemporary New River fish sampling, whichever was greater.

We constructed classification trees for *Form* in R statistical software (R Core Team, 2014) using the rpart package (Therneau, Atkinson & Ripley, 2014) and plotted the optimally pruned tree (selected using 10-fold cross-validation) using the rpart.plot package (Milborrow, 2015). To assess tree performance, we calculated a multiple-class area under the receiver operating characteristic curve (AUC) metric (Cullmann, 2015) and the overall misclassification rate. Splits were selected to minimize impurity within nodes based on the Gini index. The minimum number of observations needed to attempt a split was 10, and the minimum number of observations in any terminal node was 5.

Results

Updated status of New River stream fishes

Some updates to Jenkins & Burkhead's (1994) account of the New River fauna have accrued in the past 20 years, revising the total number of established introduced species in the New River drainage from 42 to 55, and the number of failed introductions (introduced species not reported since 1995) from six to nine (Table S1 in Supporting Information). Their late detection in the New River drainage in 1972 and 1976 respectively (Jenkins & Burkhead, 1994), and their subsequent spread, suggest that rainbow darter *Ethestoma caeruleum* and snubnose darter *E. simoterum*, which Jenkins & Burkhead (1994) regarded as probably native, were more likely introduced (M. Pinder, VDGIF, Blacksburg, personal communication). Palmer *et al*. (2006) described a putative native stock of walleye *Sander vitreus* from the New River. An updated total of 44 (43 extant) native New River species reflects the above changes. Robins (2005) formally described a ninth New River endemic, the Kanawha sculpin *Cottus kanawhae*, which Jenkins & Burkhead (1994) considered to be a subspecies of banded sculpin *C. carolinae* (However, this change does not increase the number of native New River species because *C. kanawhae* simply replaces *C. carolinae* on the New River species list).

Summary of fish-collection data set

UMNR fish collections included 77 established species, 42 (55%) of which were introduced. We excluded three introduced species, eastern mosquitofish *Gambusia holbrooki*,

redline darter *Etheostoma rufilineatum*, and highback chub *Hybopsis hypsinotus* from further analysis because they were first detected after period 7, and therefore the number of time periods having CPUE data was insufficient to fit models of spread. Thus, 74 species (39 introduced, 35 native) were retained in the final data set (Table 2.1).

There was a grand median of 2 (mean = 3.7) collections per HUC12 per time period. The median ranged from 2 to 4 (mean 2.8–5.8) across the ten time periods (Fig. S1). A grand median of 6 (mean = 7.1) non-game species were reported per collection. The median by time period ranged from 4 to 10 (mean 4.3–9.0) (Fig. S2). Fish collections were distributed fairly evenly across the UMNR for the majority of time periods (Fig. S3).

A total of 32 first detections of introduced species were reported from UMNR tributaries during the 77-year study period, which represents an average of two first detections every five years (excluding 24 unconfirmed reports). However, the rate at which first detections have accumulated (accounting for sampling effort) has decreased since the mid-20th century (Fig. 2.4).

Spreaders

We classified 31 (42%) of the 74 species as spreaders, 4 (5%) as decliners, and 39 (53%) as stable. 31% of native species were spreaders, compared to 51% of introduced species (Fig. 2.6, Table 2.1). A UMNR native, mountain redbelly dace *Chrosomus oreas*, showed the greatest average rate of spread, equivalent to a range increase of 0.71 HUC12s per year (Fig. 2.5, Table S3). Salmonids accounted for two (22%) of the nine strong spreaders, but comprised just 4% of the UMNR species pool (Fig. 2.7). Otherwise, spreaders were proportionally represented among families. Two introduced species, rainbow darter *Etheostoma caeruleum* and snubnose darter *E. simoterum* were initially classified as stable ($w_i > 0.5$ for the null model), but were reclassified as spreaders because a competing model of spread had a positive 90% LCL for β_1 and substantial AICc support ($\Delta_i = 1.7$ for *E. caeruleum* and 3.5 for *E. simoterum*).

For 26 (84%) of the 31 spreaders, including all nine strong spreaders, an exponential model (Equations 5 or 6) was most plausible (Table 2.1). However, for 14 of these exponential spreaders, the linear model was also strongly supported ($\Delta_i \leq 2$) (Table S3). The linear model (Equation 4) had the greatest support for the remaining five (16%) spreaders, three of which also showed strong support for an exponential model. Thus, 17 (55%) spreaders showed strong support for both exponential and linear models. A logistic model (Equations 7 or 8) was never

24

strongly supported. For four of the species classified as stable, an exponential model also had strong support; however, all four remained classified as stable since none had a positive 90% LCL or negative 90% UCL for β_1.

Decliners

We classified 11% of UMNR natives as decliners. No introduced species qualified as a decliner (Fig. 2.6). Cyprinids comprised 45% of the UMNR species pool, but 75% of the decliners (Fig. 2.7). Silver shiner *Notropis photogenis* showed the greatest average rate of decline, equivalent to extirpation from 0.44 HUC12s per year (Fig. 2.5, Table S3). CPUE of sharpnose darter peaked at 10.7% in period 4, but none were reported in period 10 (Fig. 2.5, Table S2).

Spread rates of introduced and native species

The regression of rate of spread against *iCPUE* with all 74 species included (Fig. 2.8, left) confirmed our results from the *Distribution trend* assignments in demonstrating that introduced species, on the average, are spreading, while most natives are in equilibrium or declining (p value for equality of slopes = 0.024, $t = 2.31$). The regression for the 40 species occupying the portion of the *iCPUE* range containing both introduced and native species (Fig. 2.8, right) showed that introduced and native species having relatively small ranges did not significantly differ in their inherent ability to spread (p value for equality of slopes = 0.341, $t = 0.97$).

Form of spread for introduced species

In the classification tree analysis of the form of spread for the 39 introduced UMNR fishes, *Form* classes Exp ($n = 16$), Lin ($n = 4$), and Sta ($n = 19$) were observed. *GensSinceDetect* ranged from 8 to 77 generations. *CPUE1* ranged from 0 to 0.32. *IntroEffort* classes 1 ($n = 13$), 2 ($n = 11$), and 3 ($n = 15$) were observed (Table S4). The optimally pruned tree had three splits on a single explanatory variable, *GensSinceDetect* (Fig. 2.9). The model misclassification rate was 28%, compared to 49% for the null model (guessing with the majority), and the multi-class AUC for the selected tree was 0.83. Exponential spreaders tended to have an intermediate number (21–31) of *GensSinceDetect*. The four linear spreaders all had *GensSinceDetect* ≥ 51. Most stable species had *GensSinceDetect* either ≥ 31 or < 21.

Spatial patterns of spread and decline

Several patterns emerged from the time-series maps for strong spreaders and decliners (Figs. S4–S16): (1) Native strong-spreaders mountain redbelly dace *Chrosomus oreas* (Fig. S4) and bluehead chub *Nocomis leptocephalus* (Fig. S5) have spread concurrently. (2) Decliners have persisted, and even spread, in certain UMNR tributary systems while declining elsewhere. The North and South forks of the New River in NC, and to a lesser extent the Little River in VA (streams labeled on Fig. 2.10), appear to have been a stronghold for decliners tonguetied minnow *Exoglossum laurae* (Fig. S7), rosyface shiner *Notropis rubellus* (Fig. S8), and silver shiner *Notropis photogenis* (Fig. S10). (3) A closer examination of the apparent upstream spread of introduced whitetail shiner *Cyprinella galactura* suggested multiple cryptic introductions upstream of a series of impassible dams (Fig. 2.10).

Discussion

Declining trend in first detections of new introduced species

Although the number of introduced stream fishes first detected in the latter half of the 20th century exceeded that of the first half in the UMNR, as was typical throughout the USA (Nico & Fuller, 1999), the rate at which new introductions are accumulating in the UMNR appears to be slowing. Elsewhere, long-term studies of temporal trends in fish invasion rates have reported a steady (Coles *et al.*, 1999; Unmack & Fagan, 2004) or increasing (Ricciardi, 2001) baseline rate of accumulation, although Cobo *et al*. (2010) noted a recent deceleration. Three hypotheses explored below invoke decreasing detectability and supply of introduced species and increasing biotic resistance to explain this pattern.

(1) *Recent introductions are harder to detect.* Early introductions in the UMNR were dominated by widespread, often officially-sanctioned stocking of large numbers of large-bodied gamefishes (e.g., common carp, centrarchids, salmonids, and ictalurids), with stocks often monitored by the state and targeted by the angling public. However, since the late 20th century, the introduction rate of new gamefish species in the UMNR has been curtailed likely due to saturation of the game species pool, declining public participation in angling (Leonard 2007), or heightened awareness of potential adverse outcomes of introductions. Thus, after a flurry of stocking novel gamefish and prey species in the 1950s–1970s (Jenkins & Burkhead, 1994), only

two new gamefish introductions (redear sunfish *Lepomis microlophus* and white perch *Morone americana*) have been reported in the UMNR since 1976.

Introductions to the UMNR in recent decades have been more cryptic due to an apparent shift in invasion pathways from intentional stocking of game and prey species to unauthorized inter-basin transfers of smaller numbers of smaller-bodied, non-game species (cyprinids, percids, and catostomids) possibly resulting from transfer and release of baitfish, release of unwanted pets, or transplanting of non-game hitchhikers on stocking trucks (M. Pinder, VDGIF, personal communication). Due to their small size, lower numbers, and non-game status, these species are much less likely to be detected until they become locally abundant or widespread. Furthermore, due to their smaller size and therefore lower dispersal ability in flowing waters (Knouft & Page, 2003), they may experience longer invasion lag times. However, the widespread adoption of more efficient fish-collection gear (electrofishing) and increased scientific collection effort in recent decades may partially mitigate for decreasing detectability of recent introductions.

(2) *The supply of new invaders is dwindling*. Each transport vector (e.g., angler) along an invasion pathway (e.g., inter-basin transfer of baitfish) brings samples from donor regions already sampled by previous vectors (Levine & D'Antonio, 2003; Lockwood *et al.*, 2007). Thus, through time, there are fewer "unsampled" candidate species available in the donor region that match the receiving environment and human preferences. Although there remain hundreds of fishes, just in the nine adjacent drainages, that have yet to colonize the New River drainage, many of them are uncommon or less susceptible to capture, or undesirable for human uses such as live bait or aquaria, and are therefore unlikely to be transplanted into the UMNR. And not all that are transported and released will be capable of becoming established in the New River drainage. However, if the sampling intensity were to increase (e.g., more anglers, or more baitfish transported per angler), the types of non-native species being imported change (e.g., preference for novel baitfish species), or the types of pathways change (e.g., increase in aquarium trade), we should expect the number of new introductions to increase (Lockwood *et al.*, 2007).

(3) *The receiving environment of the New River drainage has become increasingly resistant to new introductions*. North American fish communities, including those in the New River drainage, are commonly thought to be unsaturated with species (Jenkins & Burkhead, 1994; Angermeier & Winston, 1998; Gido & Brown, 1999; Rahel, 2002). However, as the

UMNR's species pool has grown from 35 to 79 established species, it seems intuitive that biotic resistance to newcomers has also increased, since species-rich communities are expected to use limiting resources more completely and are more likely to have competitors or predators that can exclude potential invaders (Elton, 1958). Thus, increasing biotic resistance as the receiving fish community approaches saturation is a possible explanation for the UMNR's declining invasion rate. However, evidence for the biotic resistance model in aquatic ecosystems is equivocal and is contradicted by Simberloff & Von Holle's (1999) "invasional meltdown" model, which proposes that facilitative interactions among invaders commonly lead to *increasing* invasion rates as communities accumulate introduced species (e.g., Ricciardi, 2001).

Reports of decelerating invasion rates are few, although long-term temporal studies of trends in stream-fish assemblages are uncommon. Hypotheses for the UMNR's declining invasion rate remain untested. This is an important area for future research—an improved understanding of factors that regulate invasion rates will inform management actions and advance ecological theory.

Spreaders

Salmonids were overrepresented among the spreaders in relation to their proportion of the UMNR species pool. The salmonids' apparent success is undoubtedly due in large part to high propagule pressure. Due to their status as highly esteemed gamefishes, rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* have been widely and abundantly stocked for many decades throughout the UMNR (Jenkins & Burkhead, 1994; Fuller, Nico & Williams, 1999; M. Pinder, VDGIF, personal communication; B. Tracy, NCDEQ, personal communication).

Although the spreaders were disproportionately represented by introduced species, three native minnows, mountain redbelly dace *Chrosomus oreas*, bluehead chub *Nocomis leptocephalus*, and rosyside dace *Clinostomus funduloides* were among the strongest spreaders. *Nocomis* species bury their eggs in nests the males construct of mounded gravel, and defend the nest against egg-foraging predators (Jenkins & Burkhead, 1994; Johnston, 1994a). *Nocomis* nests provide clean gravel needed for survival of developing embryos, thereby enhancing reproductive success in highly silted streams (Peoples *et al.*, 2011). Other minnows (nest associates), including mountain redbelly dace, rosyside dace, and others, also spawn on *Nocomis* nests, and

therefore benefit from clean gravel and nest defense provided by *Nocomis* hosts (Johnston, 1994a). Hitt & Roberts (2012) suggested that bluehead chub serve as a keystone species that facilitates colonization of degraded headwater streams by nest associates. This relationship is thought to be mutually beneficial, as *Nocomis* species may also benefit by reduced predation on their own eggs through the dilution effect (Johnston, 1994b; Peoples & Frimpong, 2013).

Nest association with bluehead chub hosts appears to have played a role in facilitating the rapid spread of natives mountain redbelly dace and rosyside dace and introduced saffron shiner *Notropis rubricroceus* in the UMNR. These three associates appear to have spread concomitantly with bluehead chub throughout the UMNR. All three are 'strong' (nearly obligate) *Nocomis* nest associates whose reproductive success likely relies heavily on nests and/or nest protection provided by *Nocomis* hosts (Pendleton *et al.*, 2012; Peoples & Frimpong, 2013). Pendleton *et al.* (2012) and Peoples & Frimpong (2013) found that the occurrence of strong nest associates across the middle New River drainage appeared to be dependent on nest association with *Nocomis* hosts. Nest association with bluehead chub has also been implicated in facilitating rapid expansion of an introduced minnow, rough shiner *Notropis baileyi*, in the Chattahoochee River drainage of Alabama and Georgia (Walser, Falterman & Bart, 2000; Herrington & Popp, 2004). Four other minnow species classified as strong *Nocomis* nest associates by Peoples, Blanc & Frimpong (2015) were found in the study area, including two native (white shiner *Luxilus albeolus* and rosefin shiner *Lythrurus ardens*) and two introduced species (crescent shiner *Luxilus cerasinus* and warpaint shiner *L. coccogenis*). However, the spread of these other strong associates did not appear to be as tightly linked to bluehead chub. Thus, nest association appears to be one, but not the only, mechanism driving the spread of cyprinid fishes in the UMNR.

Our reconstruction of the invasion history in the UMNR of whitetail shiner *Cyprinella galactura*, an introduced non-game spreader, indicates that multiple cryptic introductions occurred in the second half of the 20th century, which enabled their spread upstream of a series of impassible dams (Fig. 2.10). Whitetail shiners were first detected in 1954 by R.D. Ross in the headwaters of Wolf Creek in the lower portion of the UMNR (Jenkins & Burkhead, 1994). They spread rapidly throughout the lower UMNR, but for several decades appeared to be isolated below Claytor Dam 80 river km upstream of the mouth of Wolf Creek. However, in 1998 they were found at multiple sites as far as 220 river km upstream of Wolf Creek above a series of four impassable dams (Claytor, Buck, Byllesby, and Fries dams, listed in order moving upstream) on

the mainstem New River and a fifth dam on the Little River in VA. We interpret the upstream spread of whitetail shiner past five barrier dams to be the result of multiple unauthorized introductions, most likely bait-bucket releases (Fuller *et al.*, 1999). At least three independent introductions are implicated: (1) the first introduction in Wolf Creek prior to 1954; (2) at least one introduction upstream of Fries Dam prior to 1998; and (3) at least one introduction upstream of the Little River Dam prior to 1998. Telescope shiner *Notropis telescopus* exhibit a similar invasion history in the UMNR to that of whitetail shiner. They were first detected below Claytor Dam in 1958 and spread rapidly throughout suitable habitats (Jenkins & Burkhead, 1994). From 1995 to 2000 they were detected at multiple sites upstream of Claytor and Little River dams, and by 2008 they had bypassed Buck and Byllesby dams. The upstream dispersal of whitetail and telescope shiner past multiple barrier dams illustrates the role of humans in facilitating the spread of introduced species in the UMNR and the need to address unauthorized introductions before implementing a conservation strategy of retaining or installing barriers to isolate upstream natives from downstream invaders (Fausch *et al.*, 2008).

Decliners

Our study identified four native decliners in UMNR tributaries: tonguetied minnow *Exoglossum laurae*; rosyface shiner *Notropis rubellus*; silver shiner *Notropis photogenis;* and sharpnose darter *Percina oxyrhynchus*. Jenkins & Burkhead's (1994) species accounts offer possible clues as to why these four species have apparently decreased: All four are associated with clear water and seem to avoid heavy silt, and tonguetied minnows prefer cool water. Two of the decliners, tonguetied minnow and sharpnose darter, possess three of the four ecological attributes associated with extinction-prone freshwater fishes in Virginia, including small range, ecological specialization, and limited range of water sizes (Angermeier, 1995).

Silver shiner do not strongly display any extinction-prone attributes identified by Angermeier (1995), yet they were identified as the strongest decliners in our study. Silver shiner range from the Lake Erie drainage south through most of the Ohio River basin. They are considered to be highly sensitive to silt and pollution, and were extirpated from rapidly urbanizing streams near Columbus, Ohio (Miltner, White & Yoder, 2004) and appeared to be in decline throughout the southern Appalachians (Johnston *et al*., 1995). In VA, Jenkins & Burkhead (1994) described silver shiner as widespread in the New and Tennessee drainages, but

verging on extirpation in the upper Big Sandy drainage due to pervasive siltation from coal mining and hillslope agriculture.

The sharpnose darter is a riverine species found in southern tributaries to the upper and middle Ohio River, including the New and Big Sandy drainages in VA. It probes for macroinvertebrates in crevices between coarse substrates (Jenkins & Burkhead, 1994), which likely makes it vulnerable to silt deposition and embeddedness. The sharpnose darter has been recognized as a species of moderate conservation need in VA, although this designation confers no special legal status (VDGIF, 2015). Its status as a decliner in our study is tentative pending more thorough community sampling of nonwadeable tributaries and the mainstem in the UMNR, where collectors often exclusively targeted game species.

Declining CPUEs of New River natives, especially silver shiner, tonguetied minnow, and rosyface shiner, which were heretofore considered robust and secure from a conservation standpoint in the New River drainage (VDGIF, 2015), should be further investigated. Our results emphasize the importance of continuing fish-community monitoring to detect changes in fish distribution and abundance. Community sampling in nonwadeable rivers of the Virginia portion of the UMNR is especially needed. Such monitoring will also provide early detection of new introductions and increase our understanding of stream communities, effects of species introductions, and effects of other environmental changes.

The NC portion of the UMNR appears to have provided refuge to the three cyprinid decliners (rosyface shiner, silver shiner, tonguetied minnow). Since agriculture is associated with instream siltation (Berkman & Rabini, 1989; Waters, 1995; Walser & Bart, 1999), and all three cyprinid decliners are silt sensitive, this pattern may be at least partially explained by the lower percentage of agricultural land use in the NC portion than in the VA portion of the UMNR. Agricultural land use (Fry *et al*., 2011) averaged 30% for the 79 HUC12s comprising the VA portion of the UMNR and 20% for the 21 NC HUC12s. A t-test of arcsine-square-root-transformed percentages of agricultural land use for VA versus NC HUC12s was significant ($t = 3.61$, $P = 0.0007$). Mean elevation (based on Jarvis *et al.*, 2008) of the NC HUC12s was also 219 m higher than that of the VA HUC12s ($t = 9.95$, $P < 0.0001$ for log-transformed mean elevations). The higher elevation and greater forest cover of the NC watersheds likely maintain cooler water preferred by tonguetied minnow.

Alternatively, the relative stability observed in NC for the three cyprinid decliners could be an indirect result of environmental resistance to invasions. Several native and introduced spreaders including bluehead chub, mountain redbelly dace, whitetail shiner, telescope shiner, and margined madtom *Noturus insignis* were late arrivals in the NC portion of the UMNR. Delays of some spreaders in becoming widespread in the NC HUC12s could be explained by the upstream position of the NC HUC12s in the UMNR and their isolation by dams downstream. However, the success of whitetail and telescope shiner in dispersing (presumably aided by humans) upstream past multiple impassible dams suggests a limited role for dams in impeding upstream dispersal in the UMNR. Environmental resistance of the NC HUC12s offers an alternate explanation. Peoples *et al.* (2015) hypothesized that the importance of nest association increases along a gradient of physical stress. Accordingly, they found that the relative abundance and reproductive success of *Nocomis* and their strong associates increased with increasing percentage of agricultural land use. This suggests that watersheds with lower agricultural land use, such as the NC portion of the UMNR, may be less susceptible to invasion by *Nocomis* and associates. Where established, these species (especially bluehead chub and mountain redbelly dace) are typically among the most abundant UMNR tributary fishes (E. Frimpong, unpubl. data) and likely impact the receiving community through competition for limited resources. For example, Trautman (1981) noted that the tonguetied minnow rarely co-occurs with *Nocomis*. And Hitt & Roberts (2011) documented the extirpation of spawning-mound builders creek chub *Semotilus atromaculatus* and bigmouth chub *Nocomis platyrhynchus* from three UMNR streams originally surveyed by Burton & Odum (1945), while the bluehead chub and its nest associates dramatically increased their occupancy. None of the decliners are strong *Nocomis* nest associates (although tonguetied minnows construct their own pebble nests), and therefore would not be expected to directly benefit from the spread of bluehead chub. The role of bluehead chub and associates in declines of non-associate cyprinids may warrant further study.

Form of spread hypotheses

GensSinceDetect was the only explanatory variable that appeared in the optimally pruned tree for *Form*. It is not surprising that time (measured in generations) best predicted *Form*, given the strong inverse relationship between the rate of population growth and generation time (Winemiller & Rose, 1992), and that time since introduction has been recognized as an

important predictor of invasion success (Scott & Panetta, 1993; Barney & Whitlow, 2008; Catford *et al.*, 2009; although not universally—see Kolar & Lodge, 2001). The observed ranges of *CPUE1* and *IntroEffort* may have been too constrained to capture their significance in a statistical model. The misclassification rate of 28% indicates that other factors not included in our model (such as species life-history and dispersal traits and introduction site/watershed characteristics) also contribute to *Form*.

Although the lack of logistic spreaders and low sample size of linear spreaders limited our ability to explore hypotheses about form of spread, the classification tree model for *Form* provides some support for Hypothesis 1. The tree suggests that the transition from lag phase to exponential phase occurs around 21 generations after an introduced species is initially detected in UMNR tributaries. Support for a transition from the exponential to the stable phase is inconclusive, probably because few, if any, UMNR introductions have reached the stable phase (which is also a likely explanation for why a logistic model was never the best-fitting model for any species). The 19 species having *Form* = Sta could be in either lag (pre-exponential spread) or stable (post-exponential spread) phase. Final (i.e, period 10) CPUE was 6% or less for 17 of the 19. With such a limited distribution (compared to UMNR natives, 89% of which had a final CPUE $\geq$ 8%), it seems unlikely that these 17 species have undergone exponential spread. Furthermore, 13 of the 19 species having *Form* = Sta were first detected during the study period (after 1937). Exponential growth would likely have been detected had it occurred for these 13 species. A few species we classified as stable that were introduced early and have remained localized for many generations (e.g., longear sunfish *Lepomis megalotis*, yellow perch *Perca flavescens*) may be precluded from becoming widespread by unsuitable biotic or abiotic conditions in UMNR tributaries.

The 39 introduced UMNR tributary fishes exhibited three of the four hypothesized forms of spread—all but logistic. A few of the earliest introductions (e.g., smallmouth bass *Micropterus dolomieu* and common carp *Cyprinus carpio*) that we classified as stable may actually be logistic spreaders that spread rapidly and filled most of their suitable habitat prior to our study period. The four introduced species exhibiting a linear form split together at *GensSinceDetect* $\geq$ 51, which could be interpreted as evidence for a transition from exponential to stable phase. However, an exponential model was also strongly supported for three of them,

and the null model for the fourth. Therefore, evidence is weak for a change from exponential phase to stable phase at 51 generations.

We expected that *CPUE1* would help distinguish stable/linear species in lag and stable phases. However, our analyses of *Distribution trend* and spread rates suggest few UMNR introductions have reached the stable phase, which may explain why *CPUE1* did not appear in our model for *Form*. Also, the observed range of *CPUE1* may have been too constrained to capture its significance in a statistical model.

We expected that *IntroEffort* would also contribute to the tree for *Form*, as propagule pressure is widely viewed as a dominant driver of invasion success (Vermeij, 1996; Colautti & MacIssac, 2004; Marchetti *et al*., 2004; Lockwood *et al*., 2005; Ruesink, 2005; Theoharides & Dukes, 2007), although Grabowska & Przbylski (2015) found that propagule pressure did not appear to contribute to freshwater fish invasions in central Europe. Perhaps the imprecision of our three *IntroEffort* classes masked some of the effect (García-Berthou, 2007). Or perhaps *IntroEffort* is important during colonization and establishment, but plays a secondary role during the invasive spread stage.

Conclusions

We developed a quantitative framework to identify spreaders and decliners at the drainage basin scale and estimate invasion chronologies based on trends in historical presence data. In a case study of New River tributary fishes, we demonstrated how this framework has enabled further exploration, including hypothesis testing, of spatiotemporal patterns of spread and decline among introduced and native species. We found that, although the rate of new invasions appears to have declined in the UMNR since the mid-20th century: (1) The majority of fish species currently established in UMNR tributaries were introduced; (2) Over half of the introduced species are spreaders, compared to less than a third of natives; (3) Most of the spreaders (both native and introduced) still appear to be spreading exponentially; and (4) Four New River natives previously considered secure show evidence of decline.

A successful spreader must be adapted to the ecological filters of the receiving environment, as altered by human activities, and also must overcome movement barriers to access new areas. Therefore, under a separate study, we will further explore the contribution of species traits and propagule pressure to *Distribution trend* in the UMNR.

Acknowledgments

References

Akaike H. (1973) Information theory as an extension of the maximum likelihood principle. In: B.N. Petrov & F. Csaki, editors. *Second International Symposium on Information Theory*, 267–281. Akademiai Kiado, Budapest.

Angermeier P.L. (1995) Ecological attributes of extinction-prone species: Loss of freshwater fishes of Virginia. *Conservation Biology*, **9**, 143–158.

Barney J.N. & Whitlow T.H. (2008) A unifying framework for biological invasions: the state factor model. *Biological Invasions*, **10**, 259–272.

Berkman H.E. & Rabeni C.F. (1987) Effect of siltation on stream fish communities. *Environmental Biology of Fishes*, **18**, 285–294.

Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd edition. Springer-Verlag, New York.

Burton G.W. & Odum E.P. (1945) The distribution of stream fish in the vicinity of Mountain Lake, Virginia. *Ecology*, **26**, 182–194.

Clavero M. & García-Berthou E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, **20**, 110.

Cobo F., Vieira-Lanero R., Rego E. & Servia M.J. (2010) Temporal trends in on-indigenous freshwater species records during the 20th century: a case study in the Iberian Peninsula. *Biodiversity Conservation*, **19**, 3471–3487.

Cochran B. (1992) Claytor shad no accident, caller says. *Roanoke Times*, Sports section, p. C3, September 10, 1992. Available: www.roanoke.com (January 2015).

Colautti R.I. & MacIsaac H.J. (2004) A neutral terminology to define 'invasive' species. *Biodiversity Research*, **10**, 135–141.

Coles S.L., DeFelice R.C., Eldredge L.G. & Carlton J.T. (1999) Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. *Marine Biology*, **135**, 147–158.

Cullmann A.D. (2015) *HandTill2001: Multiple Class Area Under ROC Curve*. R package version 0.2-10. Available: http://CRAN.R-project.org/package=HandTill2001.

Cucherousset J. & Olden J.D. (2011) Ecological impacts of non-native freshwater fishes. *Fisheries*, **36**, 215–230.

Easton R.S. & Orth D.J. (1994) Fishes of the main channel New River, West Virginia. *Virginia Journal of Science,* **45**, 265–277.

Easton R.S., Orth D.J. & Burkhead N.M. (1993) The first collection of rudd, *Scardinius erythrophthalmus* (Cyprinidae), in the New River, West Virginia. *Journal of Freshwater Ecology,* **8**, 263–264.

Elton C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Elzhov T.V., Mullen K.M., Spiess A.N. & Bolker B. (2013) minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. R package version 1.1-8. Available: http://CRAN.R-project.org/package=minpack.lm

Fausch K.D., Rieman B.E., Dunham J.B., Young M.K. & Peterson D.P. (2008) Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology*, **23**, 859–870.

FishNet2 (2014) Fish-specimen data provided by many participating institutions via the FishNet2 portal. Available: www.fishnet2.net (July, 2014)

Froese R. & Binohlan C. (2000) Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology,* **56,** 758-773.

Fry J., Xian G., Jin S., Dewitz J., Homer C., Yang L. *et al.* (2011) Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing*, **77**, 858-864.

Fuller P.L., Nico L.G. & Williams J.D. (1999) *Nonindigenous Fishes Introduced into Inland Waters of the United States.* American Fisheries Society, Special Publication 27, Bethesda, Maryland.

García-Berthou E. (2007) The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology*, **71** (Supplement D), 33–55.

Gido, K.B & Brown J.H. (1999) Invasion of North American drainages by alien fish species. *Freshwater Biology*, **42**, 387–399.

Grabowska J., & Przbylski M. (2015) Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. *Reviews in Fish Biology and Fisheries*, **25**, 165–178.

Helfman, G. S. (2007). Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources. Island Press, Washington D.C.

Herrington S.J. & Popp K.J. (2004) Observations on the reproductive behavior of nonindigenous rough shiner, *Notropis baileyi*, in the Chattahoochee River system. *Southeastern Naturalist*, **3**, 267-276.

Hitt N.P. & Roberts J.H. (2012) Hierarchical spatial structure of stream fish colonization and extinction. *Oikos*, **121**, 127-137.

Hocutt C.H., Denoncourt R.F. & Stauffer J.R., Jr. (1979) Fishes of the Gauley River, West Virginia. *Brimleyana*, **1**, 47–80.

Hurvich C.M., & Tsai, C.L. (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Jarvis A., Reuter H.I., Nelson A. & Guevara E. (2008) Hole-filled 90-m SRTM for the globe. Available: www.arcgis.com (May 2014).

Jelks H.L., Walsh S.J., Burkhead N.M., Contreras-Balderas S., Diaz-Pardo E., Hendrickson D.A. *et al.* (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, **33**, 372–407.

Jenkins R.E. & Burkhead N.M. (1994) *Freshwater Fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.

Jennings D.P. (1988) Bighead carp (*Hypophthalmichthys nobilis*): a biological synopsis. U.S. Fish and Wildlife Service, *Biological Report*, **88**(29), 1–47.

Johnston C.E. (1994a) The benefit to some minnows of spawning in the nests of other species. *Environmental Biology of Fishes*, **40**, 213–218.

Johnston C.E. (1994b) Nest association in fishes: evidence for mutualism. *Behavioral Ecology and Sociobiology*, **35**, 379–383.

Johnston C.E., Ramsey J.S., Sobaski S.T., & Swing C.K. (1995) Introduced species of fishes in the southern Appalachians: consequences for conservation. *Journal of the Tennessee Academy of Science,* **70**, 65–76.

Jones E.B.D. III, Helfman G.S., Harper J.O. & Bolstad P.V. (1999) Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology*, **13**, 1454–1465.

Kennard M.J., Arthington A.H., Pusey B.J. & Harch B.D. (2005) Are alien fish a reliable indicator of river health? *Freshwater Biology*, **50**, 174-193.

Knouft J.H. & Page L.M. (2003) The evolution of body size in extant groups of North American freshwater fishes: speciation, size distributions, and Cope's rule. *The American Naturalist*, **161**, 413–421.

Kolar C.S. & Lodge D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.

Kolar C.S. & Lodge D.M. (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science*, **5596**, 1233–1235.

Leonard J. (2007) *Fishing and hunting recruitment and retention in the U.S. from 1990 to 2005*. U.S. Fish and Wildlife Service, Report 2001-11, Arlington, Virginia. Available: http://digitalmedia.fws.gov/cdm/ref/collection/document/id/300 (December 2015).

Lockwood J.L., Cassey P. & Blackburn T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

Lockwood J.L., Hoopes M.F. & Marchetti M.P. (2007) *Invasion Ecology*, 2nd edition. Blackwell Publishing, Oxford, UK.

Marchetti M.P., Moyle P.B. & Levine R. (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications*, **14**, 587–596.

MARIS (Multi State Aquatic Resources Information System) (2013) *Fish-collection data provided by North Carolina Wildlife Resources Commission*, North Carolina Department of Environmental Quality via www.marisdata.org (published December, 2012).

Mazerolle M.J. (2015) *AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)*. R package version 2.0-3. Available: http://CRAN.R-project.org/package= AICcmodavg.

Menhinick E.F. (1991) *The Freshwater Fishes of North Carolina*. North Carolina Wildlife Resources Commission, Raleigh.

Milborrow S. (2015) *Rpart.plot: Plot Rpart Models. An Enhanced Version of Plot.rpart*. R package version 1.5.2. Available: http://CRAN.R-project.org/package=rpart.plot

Miller R.R., Williams J.D. & Williams J.E. (1989) Extinctions of North American fishes during the past century. *Fisheries*, **14**, 22–38.

Miltner R.J., White D. & Yoder C. (2004) The biotic integrity of streams in urban and suburbanizing landscapes. *Landscape and Urban Planning*, **69**, 87–100.

Moyle P.B. & Light T. (1996) Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation*, **78**, 149–161.

Moyle P.B. & Marchetti M.P. (2006) Predicting invasion success: freshwater fishes in California as a model. *BioScience*, **56**, 515–524.

NCSM (North Carolina Museum of Natural Sciences) (2014) *Online collections: Fishes Database*. NCSM, Raleigh. Available: http://collections.naturalsciences.org/ searchFishes.aspx (July 2014).

Neely D.A. & George A.L. (2006) Range extensions and rapid dispersal of *Etheostoma blennioides* (Teleostei: Percidae) in the Susquehanna River drainage. *Northeastern Naturalist*, **13**, 391–402.

Nico L.G. & Fuller P.L. (1999) Spatial and temporal patterns of nonindigenous fish introductions in the United States. *Fisheries*, **24**, 16–27.

Olden J.D., Poff N.L. & Bestgen K.R. (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs*, **76**, 25–40.

Omernik J.M. (1987) Ecoregions of the conterminous United States. *Annals of the Association of American Geographers,* **77**, 118–125.

Page L.M. & Burr B.M. (2011) *Peterson Field Guide to Freshwater Fishes of North America North of Mexico*, 2nd edition. Houghton Mifflin Harcourt, New York, NY.

Palmer G.C., Culver M., Dutton D., Murphy B.R., Hallerman E.M., Billington N., & Williams J. (2006) Genetic distinct walleye stocks in Claytor Lake and the upper New River, Virginia. *Proceedings of the Southeast Association of Fish and Wildlife Agencies*, **60**, 125–131.

Pendleton R.M., Pritt J.J., Peoples B.K. & Frimpong E.A. (2012) The strength of *Nocomis* nest association contributes to patterns of rarity and commonness among New River, Virginia cyprinids. *American Midland Naturalist*, **168**, 202-212.

Peoples B.K., Blanc L.A. & Frimpong E.A. (2015) Lotic cyprinid communities can be structured as nest webs and predicted by the stress-gradient hypothesis. *Journal of Animal Ecology*, **84**, 1666–1677.

Peoples B.K. & Frimpong E.A. (2013) Evidence of mutual benefits of nest association among freshwater cyprinids and implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **23**, 911–923.

Peoples B.K., Tainer M.B. & Frimpong E.A. (2011) Bluehead chub nesting activity: a potential mechanism of population persistence in degraded stream habitats. *Environmental Biology of Fishes*, **90**, 379–391.

Pimentel D., Zuniga R. & Morrison D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.

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

Quinn T.J. & Deriso R.B. (1999) *Quantitative Fish Dynamics*. Oxford University Press, New York.

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org/.

Rahel F.J. (2002) Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*, **33**, 291–315.

Rejmánek M., Richardson D.M., Barbour M.G., Crawley M.J., Hrusa G.F., Moyle P.B. *et al.* (2002) Biological invasions: politics and the discontinuity of ecological terminology. *Bulletin of the Ecological Society of America*, **83**, 131–133.

Richardson D.M., Pysek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Richardson F.R. & Carnes W.C. (1964) *Survey and Classification of the New River and Tributaries, North Carolina*. Final Report, Federal Aid in Fish Restoration, Job I-O, Project F-14-R. North Carolina Wildlife Resources Commission, Raleigh.

Robins C.R. (2005) *Cottus kanawhae*, a new cottid fish from the New River system of Virginia and West Virginia. *Zootaxa*, **987**, 1–6.

Rosebery D.A. (1951). Fishery management of Claytor Lake, an impoundment on the New River in Virginia. *Transactions of the American Fisheries Society*, **80**, 194-209.

Ruesink J.L. (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology*, **19**, 1883–1893.

Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A. *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology, Evolution, and Systematics*, **32**, 305–332.

Scott M.C. & Helfman G.S. (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, **26**, 6–15.

Scott J.K. & Panetta F.D. (1993) Predicting the Australian weed status of southern African plants. *Journal of Biogeography*, **20**, 87–93.

SFCAP (Stream Fish Community Assessment Program) (2014) North Carolina Department of Environmental Quality, Division of Water Resources, Raleigh. Available: http://portal.ncdenr.org/web/wq/ess/bau/ncibi-data (June 2014)

Simberloff D. & Von Holle B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Simley J.D. & Carswell Jr W.J. (2009) The national map–hydrography. *U.S. Geological Survey Fact Sheet 2009-3054*.

Starnes W.C. & Hogue G.M. (2011) *Curation and Databasing of Voucher Collections from the North Carolina Wildlife Resources Commission 1960s Statewide Surveys of Fishes*. Final Report to North Carolina Wildlife Resources Commission. North Carolina State Museum of Natural Sciences, Raleigh.

Theoharides K.A. & Dukes J.S. (2007) Plant invasions across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256–273.

Therneau T., Atkinson B. & Ripley B. (2014) *Rpart: Recursive Partitioning and Regression Trees*. R package version 4.1-8. Available: http://CRAN.R-project.org/package=rpart.

Trautman M.B. (1981) *The Fishes of Ohio with Illustrated Keys,* revised edition. Ohio State University Press, Columbus.

Unmack P.J. & Fagan W.F. (2004) Convergence of differentially invaded systems toward invader-dominance: time-lagged invasions as a predictor in desert fish communities. *Biological Invasions*, **6**, 233–243.

USEPA (U.S. Environmental Protection Agency) (2013) *EMAP Surface Waters Data: Mid-Atlantic Streams* (1993–1996 and 1997–1998 data sets). U.S. EPA NHEERL Western

Ecology Division, Corvallis, Oregon. Available: www.epa.gov/emap/html/data/index.html (December, 2013)

Vacher K.A., Killingbeck K.T. & August P.V. (2007) Is the relative abundance of nonnative species an integrated measure of anthropogenic disturbance? *Landscape Ecology*, **22**, 821–835.

VAFWIS (Virginia Fish & Wildlife Information Service) (2013) Virginia Department of Game & Inland Fisheries, Richmond. Available: http://www.vafwis.org/fwis (October, 2013)

VDGIF (Virginia Department of Game and Inland Fisheries) (2015) Species of greatest conservation need. Appendix A In: *Virginia's 2015 Draft Wildlife Action Plan*, Henrico. http://www.bewildvirginia.org/wildlife-action-plan/draft/ (December 2015).

Vermeij G.J. (1996) An agenda for invasion biology. *Biological Conservation*, **78**, 3–9.

Walser C.A. & Bart H.L. (1999) Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River system. *Ecology of Freshwater Fish*, **8**, 237–246.

Walser C.A., Falterman B. & Bart H.L., Jr. (2000) Impact of introduced rough shiner (*Notropis baileyi*) on the native fish community in the Chattahoochee River system. *American Midland Naturalist*, **144**, 393-405.

Walters D.M., Blum M.J., Rashleigh B., Freeman B.J., Porter B.A. & Burkhead N.M. (2008) Red shiner invasion and hybridization with blacktail shiner in the upper Coosa River, USA. *Biological Invasions*, **10**, 1229–1242.

Waters T.F. (1995) Sediment in Streams: Sources, Biological Effects and Control. *American Fisheries Society Monograph 7*, Bethesda, Maryland.

Wikramanayake E.D. (1990) Conservation of endemic rain forest fishes of Sri Lanka: results of a translocation experiment. *Conservation Biology*, **4**, 32–37.

Winemiller K.O. & Rose K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2196–2218.

Yonekura R., Kawamura K. & Uchii K. (2007) A peculiar relationship between genetic diversity and adaptability in invasive exotic species: bluegill sunfish as a model species. *Ecological Research*, **22**, 911–919.

Table 2.1 *Distribution trend* and best model of spread for 74 fishes of upper and middle New River tributaries. Six models (null; linear = lin; 2-parameter exponential = exp2; 3-parameter exponential = exp3; 3-parameter logistic = log3; 4-parameter logistic = log4) were fitted to the catch-per-unit-effort time series by species (Table S2). Each species was classified as *spreader*, *decliner*, or *stable* based on Akaike's Information Criterion corrected for small samples (AICc) and 90% confidence limits on the slope/growth-rate term (β_1) of the fitted models (*Methods*, Table S3). Spreaders were split into *weak* and *strong* classes based on β_1 of the linear model. Introduced species are indicated by "*".

Species	Code	Best model	
Chrosomus oreas (mountain redbelly dace)	ChOrea	exp2	STRONG SPREADER
Clinostomus funduloides (rosyside dace)	ClFund	exp2	
Nocomis leptocephalus (bluehead chub)	NoLept	exp3	
Notropis rubricroceus (saffron shiner)*	NoRubr	exp2	
Salmo trutta (brown trout)*	SaTrut	exp2	
Oncorhynchus mykiss (rainbow trout)*	OnMyki	exp2	
Ambloplites rupestris (rock bass)*	AmRupe	exp2	
Lepomis auritus (redbreast sunfish)*	LeAuri	exp2	
Etheostoma caeruleum (rainbow darter)*	EtCaer	exp2	
Campostoma anomalum (central stoneroller)	CaAnom	exp2	WEAK SPREADER
Exoglossum maxillingua (cutlips minnow)*	ExMaxi	exp2	
Cyprinella galactura (whitetail shiner)*	CyGala	exp2	
Luxilus coccogenis (warpaint shiner)*	LuCocc	exp3	
L. cerasinus (crescent shiner)*	LuCera	exp2	
Notropis leuciodus (Tennessee shiner)*	NoLeuc	exp2	
N. chiliticus (redlip shiner)*	NoChil	lin	
N. telescopus (telescope shiner)*	NoTele	lin	
Thoburnia rhothoeca (torrent sucker)*	ThRhot	exp2	
Ameiurus nebulosus (brown bullhead)*	AmNebu	exp2	
Noturus insignis (margined madtom)	NoInsi	exp2	
Cottus bairdii (mottled sculpin)	CoBair	exp2	
Micropterus punctulatus (spotted bass)*	MiPunc	exp2	
M. salmoides (largemouth bass)*	MiSalm	exp2	
Lepomis cyanellus (green sunfish)	LeCyan	exp2	
Percina gymnocephala (Appalachia darter)	PeGymn	exp2	
P. roanoka (Roanoke darter)*	PeRoan	lin	
Etheostoma kanawhae (Kanawha darter)	EtKana	exp3	
E. simoterum (snubnose darter)*	EtSimo	lin	
E. nigrum (Johnny darter)	EtNigr	lin	
E. olmstedi (tessellated darter)*	EtOlms	exp2	
E. flabellare (fantail darter)	EtFlab	exp2	
Exoglossum laurae (tonguetied minnow)	ExLaur	exp2	DECLINER
Notropis rubellus (rosyface shiner)	NoRube	exp2	
N. photogenis (silver shiner)	NoPhot	exp2	
Percina oxyrhynchus (sharpnose darter)	PeOxyr	lin	

-continued-

Table 2.1 Page 2 of 2.

Species	Code	Best model	
Amia calva (bowfin)*	AmCalv	null	
Esox niger (chain pickerel)*	EsNige	null	
Cyprinus carpio (common carp)*	CyCarp	null	
Carassius auratus (goldfish)*	CaAura	null	
Notemigonus crysoleucas (golden shiner)*	NoCrys	null	
Rhinichthys cataractae (longnose dace)	RhCata	null	
R. atratulus (blacknose dace)	RhAtra	null	
Semotilus atromaculatus (creek chub)	SeAtro	null	
Nocomis platyrhynchus (bigmouth chub)	NoPlat	null	
Phenacobius teretulus (Kanawha minnow)	PhTere	null	
Cyprinella spiloptera (spotfin shiner)	CySpil	null	
Luxilus albeolus (white shiner)	LuAlbe	null	
L. chrysocephalus (striped shiner)	LuChry	null	
Lythrurus ardens (rosefin shiner)	LyArde	null	
Notropis hudsonius (spottail shiner)*	NoHuds	null	
N. scabriceps (New River shiner)	NoScab	null	
N. volucellus (mimic shiner)	NoVolu	null	
N. procne (swallowtail shiner)*	NoProc	null	STABLE
Pimephales promelas (fathead minnow)*	PiProm	null	
P. notatus (bluntnose minnow)	PiNota	null	
Hypentelium nigricans (Northern hogsucker)	HyNigr	null	
Moxostoma cervinum (blacktip jumprock)*	MoCerv	null	
Catostomus commersonii (white sucker)	CaComm	null	
Ictalurus punctatus (channel catfish)	IcPunc	null	
Ameiurus natalis (yellow bullhead)*	AmNata	null	
A. melas (black bullhead)*	AmMela	null	
Salvelinus fontinalis (brook trout)	SaFont	null	
Cottus kanawhae (Kanawha sculpin)	CoKana	null	
Pomoxis nigromaculatus (black crappie)*	PoNigr	null	
P. annularis (white crappie)*	PoAnnu	null	
Micropterus dolomieu (smallmouth bass)*	MiDolo	null	
Lepomis megalotis (longear sunfish)*	LeMega	null	
L. macrochirus (bluegill)*	LeMacr	null	
L. gibbosus (pumpkinseed)*	LeGibb	null	
L. microlophus (redear sunfish)*	LeMicr	null	
Perca flavescens (yellow perch)*	PeFlav	null	
Percina caprodes (logperch)	PeCapr	null	
Etheostoma osburni (candy darter)	EtOsbu	null	
E. blennioides (greenside darter)	EtBlen	null	
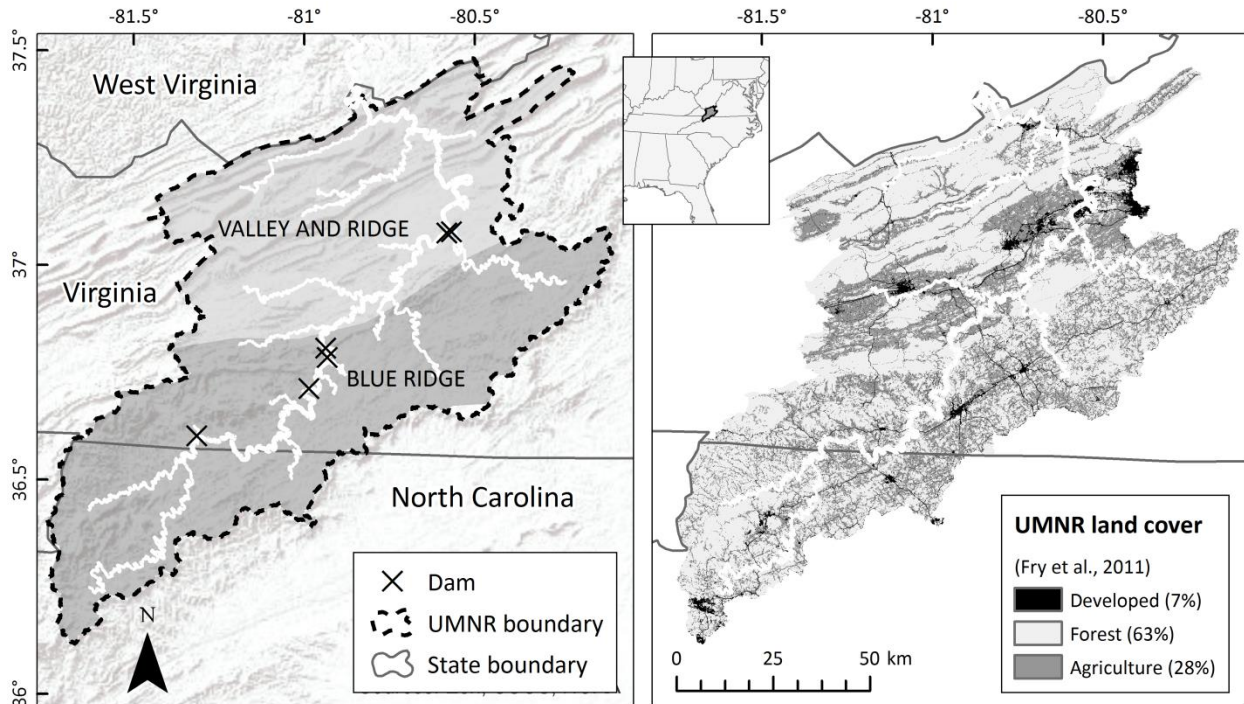
Fig. 2.1 The upper and middle New River (UMNR) study area comprised the Virginia and North Carolina portions of the New River drainage. Left map shows physiographic provinces and major dams. Right map shows 2006 land cover *sensu* Fry *et al.* (2011).
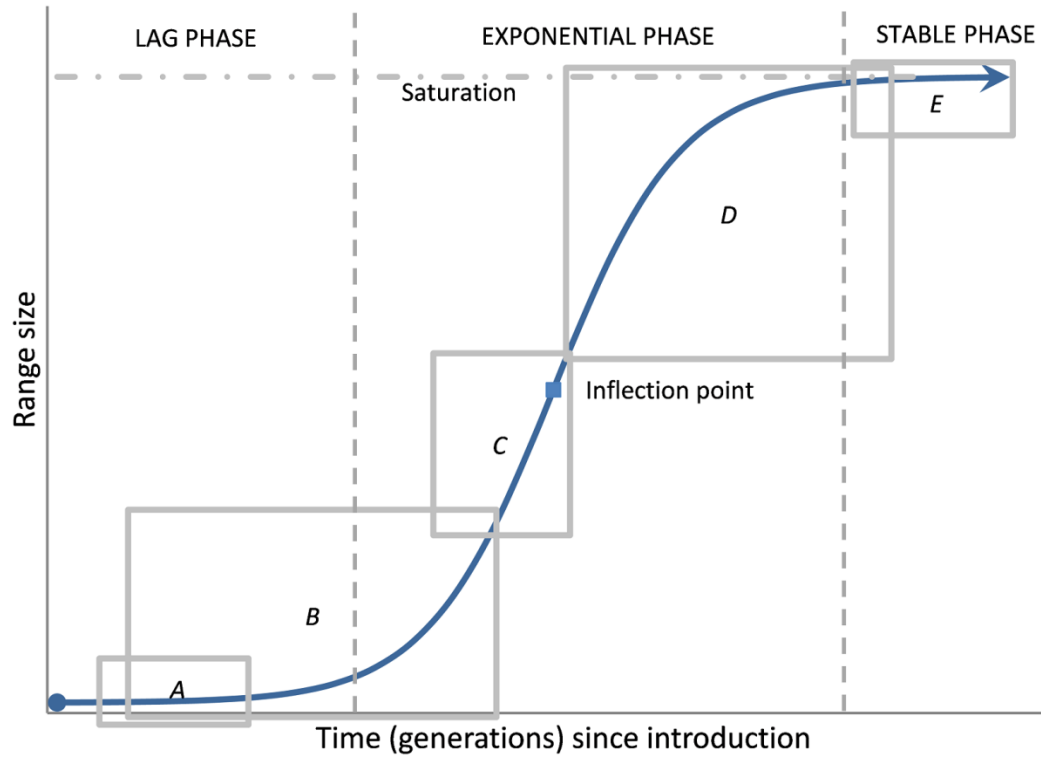
Fig. 2.2 Logistic pattern of spread for an idealized invasion. Depending on which phase of the underlying logistic growth curve is sampled, an invasion may exhibit an exponential (Area B), rapidly rising linear (C), stable or slowly rising linear (A, E), or logistic (D) form of spread.
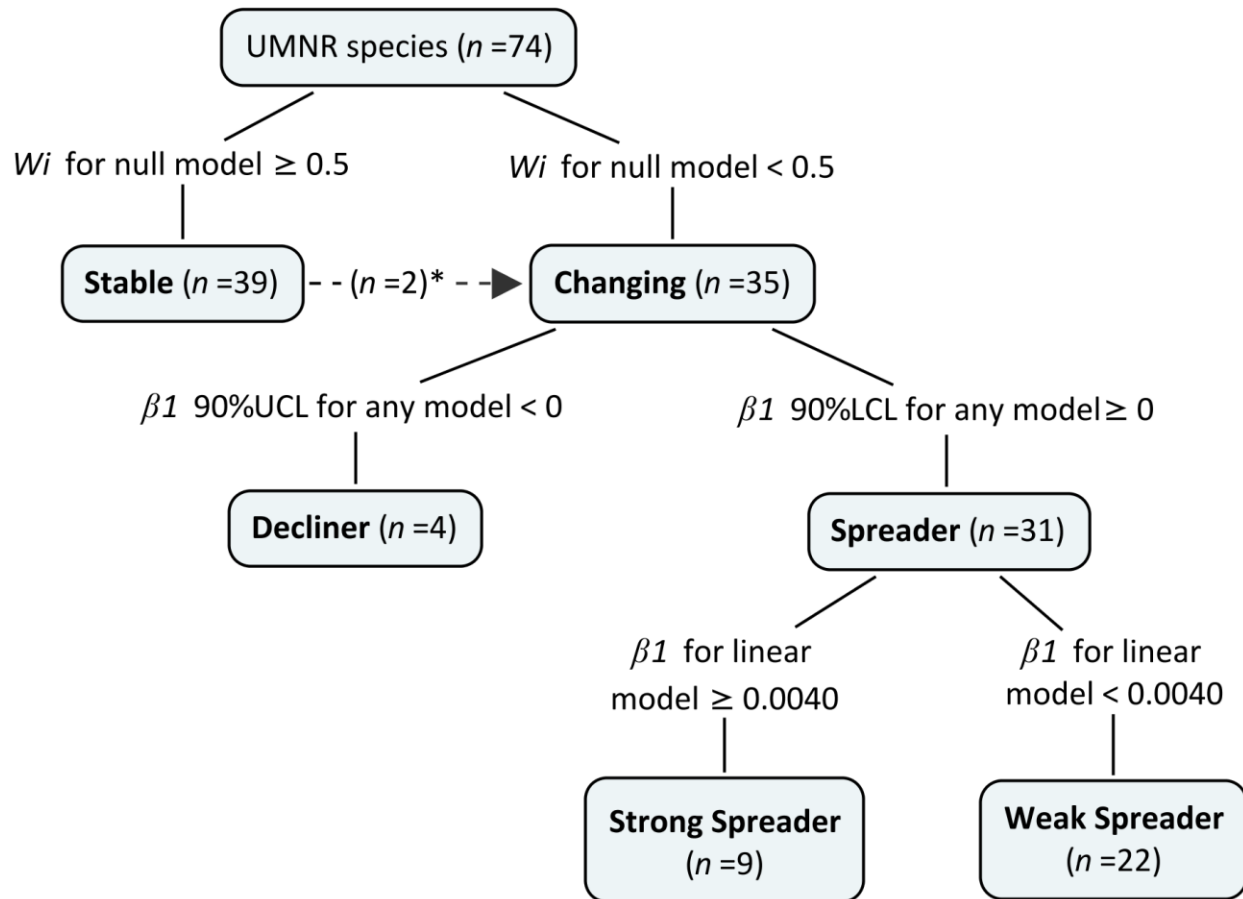
Fig. 2.3 Method used to classify spreader status of fishes of upper and middle New River (UMNR) tributaries. See Equations 3–8 for models of spread/decline being compared. Wi = Akaike model weight. $\beta1$ = slope/growth-rate term estimated from regressions of catch per unit effort (Equation 1) against time. UCL/LCL = upper/lower confidence limits for $\beta1$.

* We screened the stable group for species that would otherwise qualify as spreaders or decliners based on $\beta1$ confidence limits and considered moving them from the stable group to spreaders or decliners based on $AICc_i - AICc_{min}$ (Δ_i), where: AICc = Akaike's Information Criterion corrected for small samples; $AICc_i$ = AICc for model i; $AICc_{min}$ = lowest AICc across all models. Competing models having $\Delta_i \leq 7$ are plausible (Burnham & Anderson, 2002).
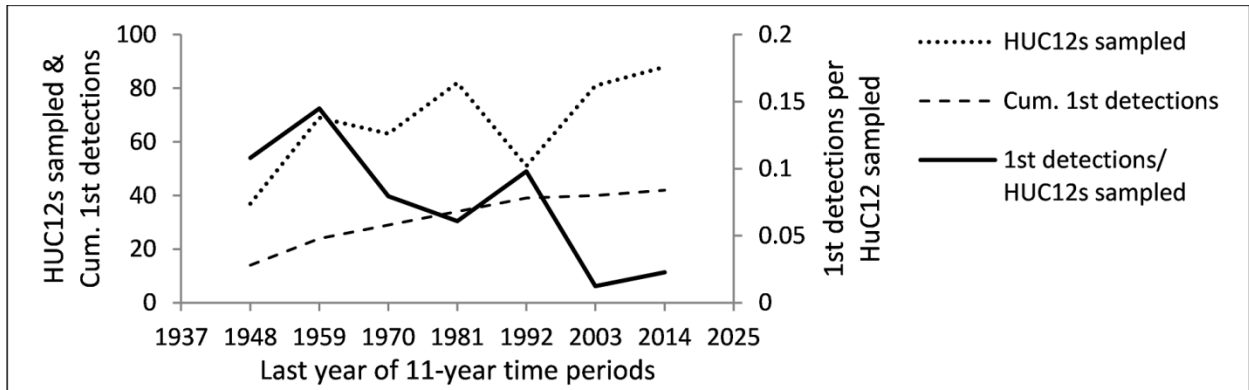
Fig. 2.4 Trend in frequency of first detections of introduced fishes in upper and middle New River tributaries. Observations were binned in seven 11-year periods, with the first period ending in 1948. "HUC12s" in the *y*-axis labels stands for sixth-level hydrologic units (subwatersheds).
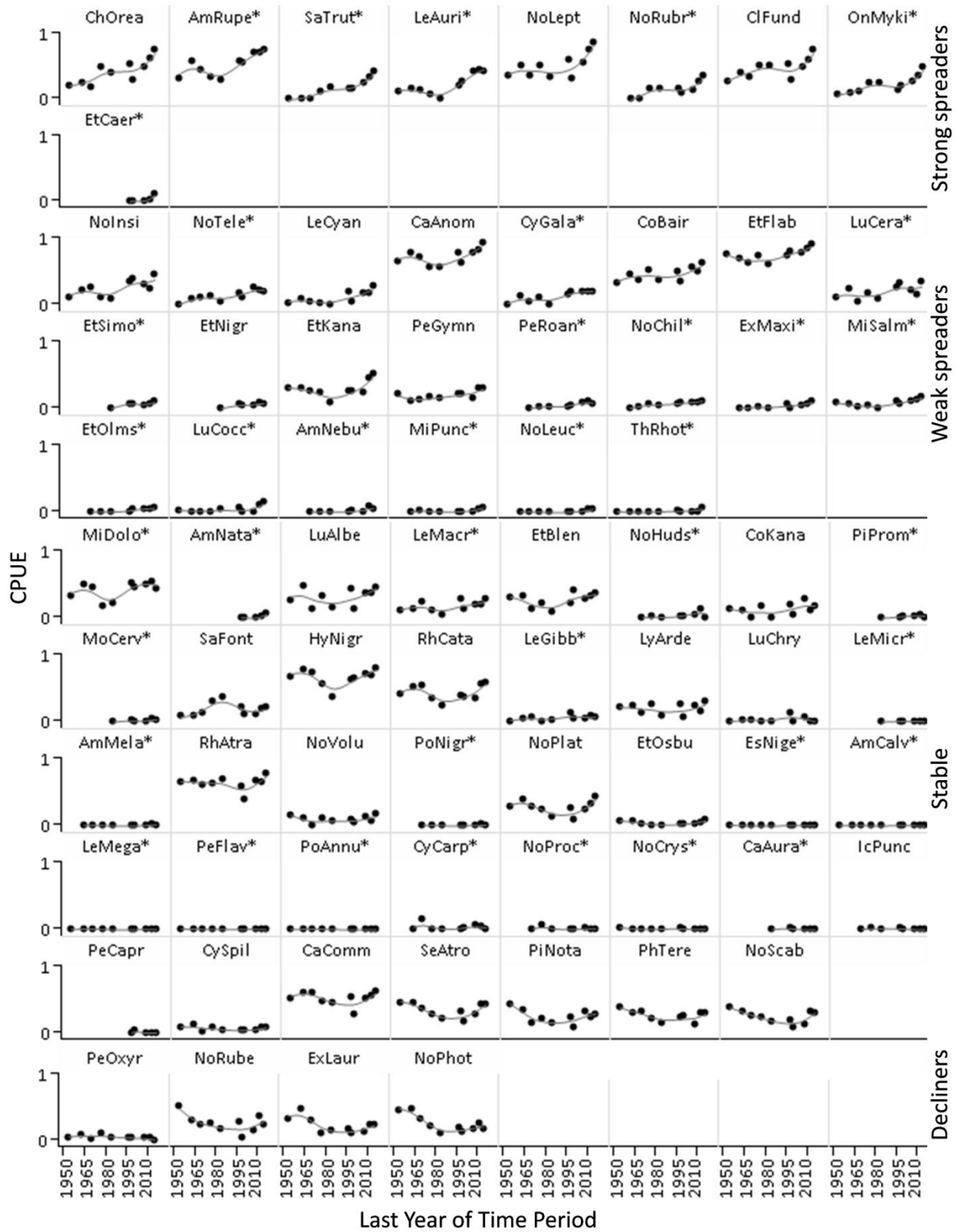
Fig. 2.5 Scatter plots of catch per unit effort (CPUE) versus time for 74 fishes of upper and middle New River tributaries. A smoothed trend line is shown. Introduced species are indicated by "*". Species codes are defined in Table 2.1.
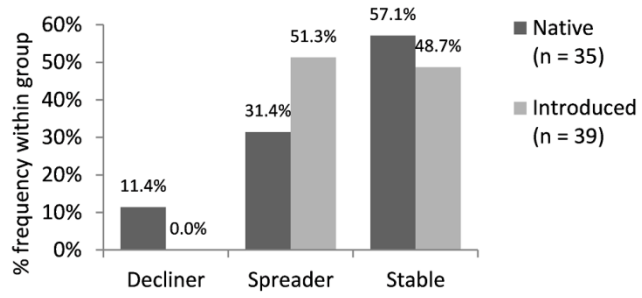
Fig. 2.6 Relative frequency of *Distribution trend* classes for 39 introduced and 35 native fishes of upper and middle New River tributaries.
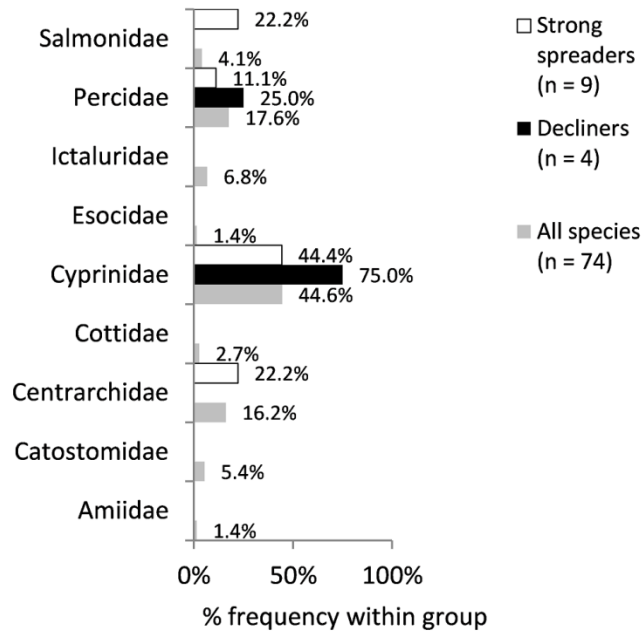
Fig. 2.7 Relative frequency of strong spreaders and decliners among fish families of upper and middle New River tributaries.
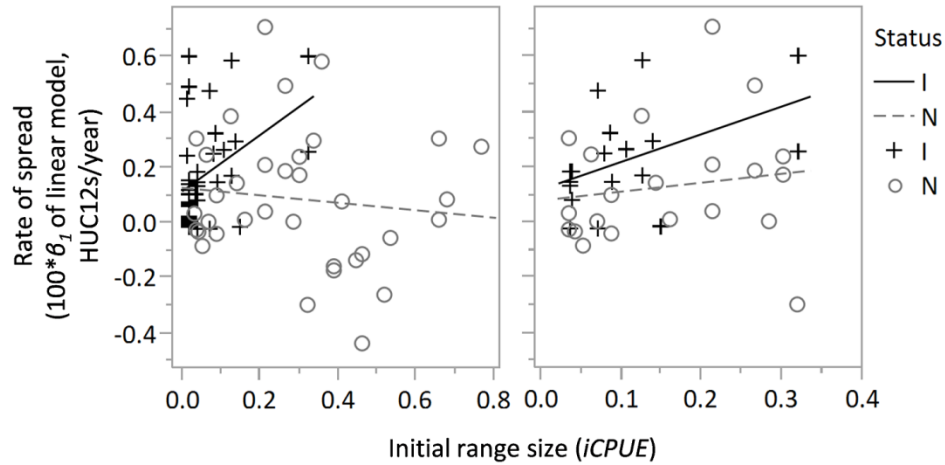
Fig. 2.8 Comparison of spread rates of introduced (I) and native (N) fishes in upper and middle New River tributaries, controlling for initial range size (*iCPUE*, first non-zero catch per unit effort in the time series). "HUC12s" in the *y*-axis label stands for sixth-level hydrologic units (subwatersheds). The regression with all 74 species included (left) shows that introduced species, on the average, are spreading, while natives are in equilibrium (*p* value for equality of slopes = 0.024). The regression for the 40 species occupying the portion of the *iCPUE* range containing both introduced and native species (right) shows that introduced and native species did not significantly differ in their inherent ability to spread (*p* value for equality of slopes = 0.341).
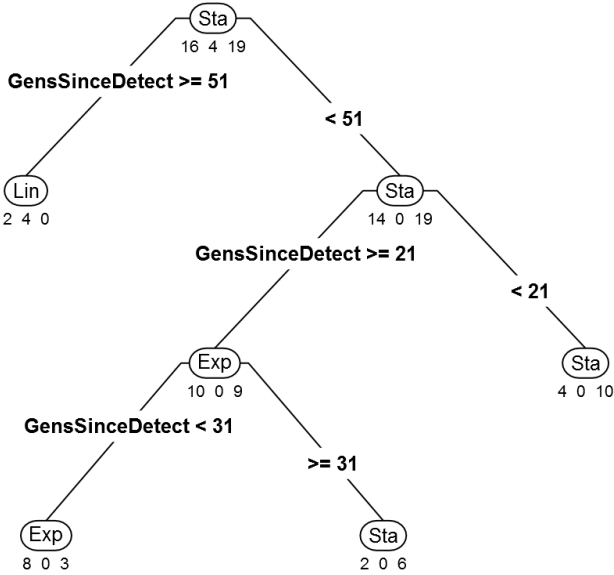
Fig. 2.9 Classification tree analysis of the form of spread exhibited by the 39 introduced upper and middle New River (UMNR) tributary fishes during the 77-year study period. The response variable *Form* had three nominal classes "Exp" = exponential, "Lin" = linear, "Sta" = stable. A fourth logistic form was not observed. The three explanatory variables (only one of which appears in the optimally pruned tree) were generations since first detected *GensSinceDetect* (continuous, ranging from 8 to 77 generations); initial catch per unit effort *CPUE1*; and propagule pressure *IntroEffort* (see *Methods*). Each split is labeled with the values of the explanatory variable that determined the split. Each node is labeled with the predicted *Form* class (inside oval) and the distribution of the observed values (Exp, Lin, Sta) (under oval). The misclassification rate of the model was 28%, compared to 49% for the null model (guess with the majority), and the multi-class area under the receiver operating characteristic curve (AUC) was 0.83. The tree was plotted using the rpart.plot package (Milborrow, 2015).
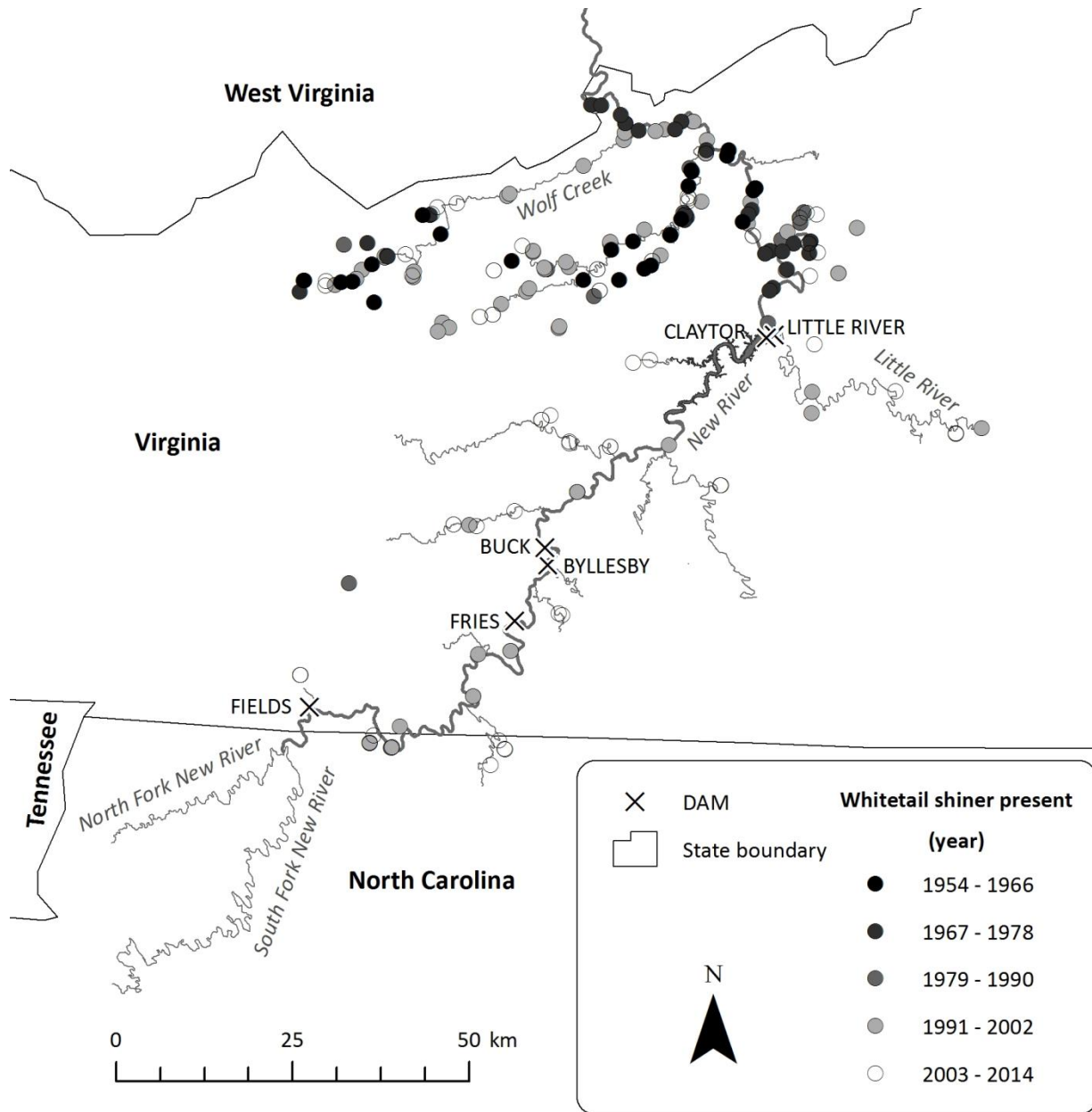
Fig. 2.10 Whitetail shiner *Cyprinella galactura* distribution map in the upper and middle New River drainage. This spreader was first detected in 1954 in the Wolf Creek headwaters (Jenkins & Burkhead, 1994). Subsequent detections of whitetail shiner upstream of a series of impassible dams on the New and Little rivers suggest at least three unauthorized introductions occurred: (1) Wolf Creek prior to 1954; (2) upstream of Fries Dam prior to 1998; (3) upstream of Little River Dam prior to 1998.

CHAPTER 3: SPECIES TRAITS PREDICT STREAM-FISH INVADERS IN AN
APPALACHIAN (USA) DRAINAGE BASIN

Running title: Traits predict invasion

Keywords: boosted classification trees, colonization, disturbance, ecological filters, invasive
species, spread, traits

53

Summary

1. Fish invasions imperil native fauna, cause substantial economic losses, and present opportunities to advance ecological theory. Yet species traits and human activities mediating stream-fish invasions remain poorly understood.

2. We compared the influence of biological traits (morphology, physiology, reproduction, and life-history traits) versus ecological traits (geographic distribution, habitat association, food habits) on invasion success of native and introduced stream fishes during the colonization and spread stages in an Appalachian (USA) drainage basin. Our findings suggest that biological traits are not only more amenable to mechanistic interpretation than ecological traits, but also more predictive of species invasiveness.

3. Colonization success was positively related to time since introduction, 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. Explanatory variables estimating human use and propagule pressure were unrelated to invasion success.

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

5. Our findings suggest that: biological traits may be more useful than ecological traits in predictions and mechanistic interpretations of invasiveness; biotic factors such as parental care and nest association can act as key invasion drivers over large spatial scales; native invaders should not be overlooked; and analysis of a comprehensive suite of species traits can reveal potential mechanisms mediating invasions and highlight opportunities to bolster invasion resistance.

Introduction

A better understanding of biological invasions is important for practical and conceptual reasons (García-Berthou, 2007). Applications requiring accurate knowledge of factors leading to successful invasions include managing harmful invasive species, sustaining desirable species, and assessing risks and benefits prior to future introductions. In North America, as globally, invasions are thought to be among the leading causes of extinction of freshwater fishes (Miller, Williams & Williams, 1989; Clavero & García-Berthou, 2005; Helfman, 2007). Invasions can

54

also be expensive—a net annual economic loss of $5.4 billion was attributed to invasive fishes in the USA (Pimentel, Zuniga & Morrison, 2005). Conceptually, invasions serve as "experiments in nature" (Grinnell, 1919) for testing ecological and evolutionary theories and examining community responses to environmental change (Vermeij, 1996; Sakai *et al.*, 2001; Olden, Poff & Bestgen, 2006; Sax *et al.*, 2007). Since a successful invasion requires a match between an invader and the receiving environment, it is important to understand which characteristics (species traits) of invaders mediate their capacity to become invasive (invasiveness). By quantitatively examining species traits of successful invaders, we can improve our ability to predict and control invasions and identify and more strategically address human practices that have facilitated invasions.

Invasion process

The invasion process is commonly understood as a series of stages (Williamson, 1996), each having distinct ecological filters/barriers (Richardson *et al.*, 2000; Blackburn *et al.*, 2011), a species encounters in a new environment while expanding beyond its initially low population density. Theoharides & Dukes (2007) described four invasion stages (Fig. 3.1): (1) Transport.–Human-assisted movement of fish to a new location outside of their natural range. (2) Colonization.–Survival of transplanted individuals. (3) Establishment.–Successful reproduction and the development of self-sustaining populations. (4) Spread.–Dispersal from source populations resulting in the establishment of new populations outside of the area where first introduced. Establishment is the most studied stage for fish invasions, but little data is available for stages before and after establishment, or on impacts to native species (García-Berthou, 2007).

Invasion drivers

Interacting factors (drivers) including ecological filters, human activities, and invader traits contribute to (or impede) invasions. Ecological filters define the susceptibility of the receiving environment to invasion (its invasibility; Drake *et al.*, 1989). The biotic-abiotic-movement (BAM) diagram (Peterson *et al.*, 2011) helps clarify the role of ecological filters in the invasion process (Fig. 3.2). The distributional area of a species comprises the intersection of three zones defined by characteristic ecological filters: areas where **B**iotic interactions with other species are favorable; areas where **A**biotic conditions and resources are suitable; and areas into

which access (**M**ovement) has been provided. An invasion can occur when humans facilitate the spread of a species from its occupied area into an invadeable area (i.e., a new area having biotic and abiotic ecological filters to which the species is adapted).

Humans enable (or impede) invasions either directly by transporting species across biogeographic barriers, or indirectly through changes to abiotic or biotic characteristics of the receiving environment that alter its invasibility. Novel conditions due to human land-use practices may facilitate the expansion of native, as well as introduced invaders into areas that were previously unsuitable. Examples include the rapid spread of introduced equilibrium strategists (Winemiller & Rose, 1992) following a century of dam-building in the Colorado River basin (Olden *et al.*, 2006), a greater number of established introductions in montane than in lowland watersheds of the Mid-Atlantic region (USA) attributed in part to creation of novel lentic habitats (Lapointe, Thorson & Angermeier, 2012), and "native invasions" of deforested Appalachian highland streams (Scott & Helfman, 2001) and lowland tropical headwaters (Lorion & Kennedy, 2009) by native fishes normally found further downstream in the same drainage basin.

A successful invader must be adapted to the dominant ecological filters of the receiving area. An organism's adaptations to its environment are described in terms of species traits (Frimpong & Angermeier, 2010). Different suites of ecological filters may be influential during each stage of an invasion (Vermeij, 1996; Kolar & Lodge, 2001); therefore, species traits that enable or deter invasions may also vary between stages (Kolar & Lodge, 2001; Kolar & Lodge, 2002; Marchetti, Moyle & Levine, 2004; Theoharides & Dukes, 2007) (Fig. 3.1). Species traits of fishes have been categorized into four major domains of *biological traits* (morphology, reproduction, physiology, life-history), and three domains of *ecological traits* (trophic, geographic distribution, habitat preference) linked to performance (capacity to maintain biomass over many generations) and fitness (lifetime reproductive success) (Frimpong & Angermeier, 2010).

Biological traits are innate (not dependent on proximate environmental filters in which the species is observed) physiological requirements, morphological adaptations, and life-history tactics that have evolved in response to ultimate environmental factors over evolutionary time scales (Vieira *et al.*, 2006; Frimpong & Angermeier, 2010). Biological traits can provide mechanistic explanations for a species' response to the environment but may be phylogenetically

constrained (Poff *et al.*, 2006). Ecological traits describe an organism's environmental preferences and associated behaviors (Vieira *et al.*, 2006), and are therefore indirect expressions of biological traits (Frimpong & Angermeier, 2010). Ecological traits are more sensitive than biological traits to proximate environmental filters, and therefore less tied 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). For mechanistic interpretations in trait-based approaches, a recommended approach is to find biological traits that drive an organism's ecological behaviors, while accounting quantitatively for relatedness (Frimpong & Angermeier, 2010).

Life-history strategies comprise suites of biological traits that mediate trade-offs between survival and reproduction in different environments (Winemiller & Rose, 1992). The fish life-history model of Winemiller & Rose (1992) (hereafter W&R model) extends the classic *r–K* model (Pianka, 1970) by splitting the *r* strategy into *periodic* and *opportunistic* strategies and redefining the *K* strategy as the *equilibrium* strategy. Thus, the W&R model describes a triangular continuum having three end-point strategies resulting from trade-offs among fecundity, juvenile survival, and generation time (Fig. 3.3). A species' position in W&R space represents an adaptive response to gradients in spatiotemporal scale and predictability of environmental variability. Opportunistic strategists, in response to frequent, unpredictable disturbances (e.g., upstream reaches of temperate streams), adopt a colonizing strategy typified by short generation time, small body size and low fecundity, serial spawning, and low parental care. Periodic strategists (long generation time, large body size and fecundity, low parental care) are adapted to habitats having large-scale, predictable patterns of environmental variation (e.g., large, temperature floodplain rivers). Stable habitats (e.g., regulated rivers, lakes, tropical climate) or chronic competition or stress favor equilibrium strategists (low fecundity, large eggs, or parental care) due to their emphasis on juvenile survival over fecundity, which confers competitive advantages in density-dependent situations where biotic interactions play a larger role (Winemiller, 2005).

Human factors related to introduction purpose and effort ("introduction attributes"), in addition to species traits and watershed characteristics/alteration, strongly influence invasion success. Propagule pressure (the number of individuals released combined with number of release events; Lockwood *et al.*, 2005) is recognized as a key human-mediated invasion driver

(Marchetti *et al.*, 2004; Catford *et al.*, 2009), albeit a difficult factor to estimate accurately, especially for fishes (García-Berthou, 2007). Secondly, since human (e.g., anglers, fishery managers, aquarists) preferences largely dictate which species are intentionally introduced, as well as mediate propagule pressure, predictors related to human use of a species (e.g., none, gamefish, baitfish, commercial) can contribute to models of fish invasion outcomes (Ruesink, 2005; Alcaraz, Vila-Gispert & García-Berthou, 2005). Finally, since the invasion process and its drivers (e.g., propagule pressure, population growth rate) vary through time, time since introduction may be an important predictor of invasion success (Scott & Panetta, 1993; Ruesink, 2005; Vila-Gispert, Alcaraz & García-Berthou, 2005; Barney & Whitlow, 2008; Catford *et al.*, 2009), although perhaps not universally—see Kolar & Lodge, 2001 & 2002).

From prior studies of invader traits we have learned to address invasion stages independently, include key introduction attributes other than species traits (e.g., propagule pressure, human uses, time since introduction), and control for the lack of statistical independence among species (Gido & Brown, 1999; Kolar & Lodge, 2002; Marchetti *et al.*, 2004; Lockwood *et al.*, 2005; Ruesink, 2005; García-Berthou, 2007; Catford *et al.*, 2009). García-Berthou (2007) compared ten quantitative fish invasiveness studies from North America (California, Colorado, the Great Lakes) and Europe (Iberian Peninsula) plus two global studies and identified the following research needs: investigation of invasion stages other than establishment; more precise measures of propagule pressure; data from different geographic regions; comparison of native and invasive species; and use of comprehensive traits data sets (a median of 10.5 predictors were included in the 12 studies reviewed). Furthermore, we note that prior invasiveness studies comparing natives to non-natives, or successful versus failed non-native invaders, have overlooked intra-basin native invasions, which provide an early indication of impairment (Scott & Helfman, 2001) and bolster sample size in models of invasion success.

While meeting the research needs identified above, the present study quantitatively examines species traits and introduction attributes of native and introduced invasive fishes in tributaries of the New River drainage basin (central Appalachian Mountains, USA) during the colonization and spread stages. We first compiled a dataset of 49 species traits and introduction attributes for the 74 native and introduced stream fishes analyzed in Chapter 2 of this thesis. Then we addressed the following questions: (1) Do strong colonizers and spreaders share traits that consistently differentiate them from weak colonizers and nonspreaders? (2) Do influential

species traits differ between colonization and spread stages? (3) How important are introduction attributes (propagule pressure, time since introduction, game/non-game status) compared to biological and ecological species traits in influencing invasion outcomes? (4) What can we infer using a trait-based approach about dominant ecological filters shaping the New River fish assemblage?

Methods

Study area and fauna

This study was conducted in tributaries of the upper and middle portion of the New River basin of North Carolina and Virginia, USA, hereafter referred to as the UMNR (Fig. 3.4). Located in the central Appalachian Mountains, the UMNR drains approximately 10,000 km^2 of the Blue Ridge, and Valley and Ridge ecoregions (Omernik, 1987). The underlying geology is primarily igneous in the Blue Ridge and sedimentary (carbonates and shale) in the Valley and Ridge. The two hydrologic subbasins comprising the upper and middle New River have the highest average elevation (829 m and 764 m, respectively) of Virginia's 39 subbasins (based on a 90-m world digital elevation model available at www.arcgis.com).

Human activity since European settlement (deforestation, agriculture, residential development, impoundments) has transformed many Appalachian highland streams functionally into lower-elevation streams by increasing water temperature, fine sediment and nutrient inputs, and availability of lentic habitats (Jones *et al.*, 1999), creating novel conditions more suitable for generalist, silt-tolerant, warm water species, including non-native species, as well as native species that previously lived downstream (Angermeier & Winston, 1998; Scott & Helfman, 2001). Land cover in the UMNR comprises 63% forest, 28% agricultural, and 7% developed lands (Fry *et al.*, 2011; Fig. 3.4). A series of five hydroelectric dams on the mainstem New River and one on the largest UMNR tributary, Little River (Virginia), ranging in height from 4 to 42 m were constructed from 1902 to 1939 (Fig. 3.4). The largest, Claytor Dam, impounds a 34-km-long, 1819-ha mainstem reservoir (Rosebery, 1951), which, along with thousands of smaller hydroelectric, recreation, flood-control and farm impoundments in the UMNR, has been repeatedly stocked with non-native game and prey fishes over the past century.

Although the New River basin, with just 44 native fish species, is considered the most depauperate of all 26 major eastern USA drainages, it has a disproportionately large number of endemic (9, or 20%) species (Jenkins & Burkhead, 1994). The New River's depauperacy and high rate of endemism are due in large part to a barrier falls at the outlet and the montane aspect of the basin (Jenkins & Burkhead, 1994). The depauperate New River fauna included few native gamefish species. However, state-sanctioned stocking of non-native game and prey species from the mid-19th century through the 1970s, supplemented by unauthorized inter-basin transfers of baitfish since the mid-20th century, have added 55 established introduced fish species, such that the New River has the greatest proportion of introduced-to-native species (55:44) among eastern USA drainages (Jenkins & Burkhead, 1994; as updated by Chapter 2 of this thesis). These diverse introduction cases make the New River a particularly rich system for the study of stream-fish invasions in a region underrepresented in the invasion literature. Despite its distinctive fish fauna, the UMNR's introduction histories and pathways (e.g., official and illegal introductions of game- and bait-fishes), land use practices (e.g., deforestation, agriculture, impoundments), and the suite of species traits being analyzed in the present study are broadly representative of other montane, temperate drainage basins worldwide.

Fish traits and introduction attributes matrix

We compiled a matrix of UMNR species traits based primarily on the FishTraits database (Frimpong & Angermeier, 2009), Jenkins & Burkhead (1994), and other sources listed in Table S5. Traits were grouped into two major categories: biological; and ecological. All seven major trait domains defined by Frimpong & Angermeier (2010) were represented, including four domains of biological traits (life history, morphology, reproduction, and physiology) and three domains of ecological traits (geographic distribution, habitat preference, and trophic). We also compiled introduction attributes describing propagule pressure, time since introduction, and human use), the first two of which applied only to introduced species. We removed highly correlated variables (Pearson or Spearman's $| r | \geq 0.8$), keeping the variable having the most parsimonious derivation (e.g., algae or phytoplankton feeder was retained rather than herbivore or diet breadth when all three were highly correlated), or the variable that applied to more species (e.g., longitude at native range centroid was retained rather than distance from nearest native source because the latter applied only to introduced species).

Accounting for phylogenetic correlation in biological traits

Since related species are not independent sampling units (i.e., biological traits co-occur in closely related species due to common ancestry), we first needed to account for phylogenetic non-independence of biological traits among species (Felsenstein, 1985; Fisher & Owens, 2004; Alcaraz *et al.*, 2005). To do so, we used phylogenetic eigenvector regression (PVR; Diniz-Filho, Ramos de Sant'Ana & Bini, 1998), which can accommodate small sample sizes, low levels of phylogenetic correlation, varying data types, and phylogenetic uncertainty better than other methods such as Felsenstein's (1985) independent contrasts (Diniz-Filho *et al.*, 1998; Olden *et al.*, 2006). Since ecological traits can change with proximal environmental cues, they are less tied to phylogeny (Poff *et al.*, 2006); therefore the ecological traits and introduction attributes were not subjected to PVR.

PVR requires a phylogeny including all focal taxa in the study from which a phylogenetic distance matrix can be computed. Since a phylogeny for UMNR fishes did not exist, we assembled one. The topology of higher levels of the tree (order or family and above) was based on Betancur *et al.*'s (2013) tree of life of bony fishes. Lower levels (to genus) were assembled from the most recent phylogeny for each order or family that included all focal genera of this study, including: Clupeiformes (Lavoué *et al.*, 2013); Cypriniformes (Cypriniformes Commons, 2012); Ictaluridae (Hardman, 2005); Esociformes and Salmoniformes (López, Chen & Ortí, 2004; Campbell *et al.*, 2013); Centrarchidae (Roe, Harris & Mayden, 2002); Percidae (Smith *et al.*, 2014); and Cottidae (Smith & Busby, 2014). The Cypriniformes Commons (2012) tree separated New River *Notropis* species into two groups, but excluded three focal species of this study (*N. scabriceps, N. rubricroceus,* and *N. chiliticus*). Based on the sequence of species listed by Page & Burr (2011), we grouped *N. scabriceps* along with *N. telescopus, N. rubellus,* and *N. photogenis*. We grouped *N. rubricroceus* and *N. chiliticus* along with *N. chrosomus* and the other members of the *Hydrophlox* subgenus of *Notropis*.

We built a phylogenetic distance matrix for UMNR species (**D**, Table S6) by counting the pairwise number of nodes between genera (or subgeneric groupings of *Notropis* and *Luxilus*), with congeners assigned a distance value of zero. When performing PVR, phylogenetic distances between taxa are ideally expressed in terms of actual genetic distance (e.g., divergence time from the common ancestor) estimated by molecular techniques (Diniz-Filho *et al.*, 1998). However, actual genetic distances were unavailable for many focal species pairs in this study, and the

node-counting method provides an appropriate approximation of distance (Olden, Poff & Bestgen, 2008; Pendleton *et al.*, 2012).

The PVR began with a principal coordinate analysis (PCoA; Gower, 1966) to extract the eigenvalues and eigenvectors of **D** (Diniz-Filho *et al.*, 1998). Then we regressed the two significant positive eigenvectors of **D** (identified using the broken-stick method; Frontier, 1976) against each biological trait using linear regression for numeric traits and logistic regression for binary traits. Residuals from these regressions, representing phylogenetically independent traits, were then compiled into a phylogenetically-independent traits matrix (**P**) along with the raw ecological traits and introduction attributes. Ordinary residuals were obtained from linear regressions and Pearson's residuals from logistic regressions. Since values of biological traits in **P** represent PVR residuals, they no longer correspond to the same measurement scale as the original traits, but their effect on the dependent variable can still be interpreted in terms of a positive or negative response.

Contribution of species traits to invasion outcomes

We defined two binary response variables, *Colonizer* and *Spreader*, to represent invasion success in the UMNR at two points along the invasion continuum. *Colonizer* represented invasion success through the colonization stage and applied only to the 39 introduced UMNR species (Chapter 2). We divided the UMNR into three catchments with restricted interconnectivity. Two adjacent upstream catchments (one upstream of Claytor Dam, the other upstream of Little River Dam) were each isolated from the downstream catchment (downstream of Claytor Dam) by a major dam and reservoir such that in-river movement of introduced fish or their propagules between catchments was impossible in the upstream direction and highly unlikely in the downstream direction. Thus, occurrence of an introduced species in multiple catchments required multiple human-aided colonization events. Introduced species reported from 1–2 catchments were classified as weak colonizers, and those reported from all three catchments as strong colonizers. We summarized species occurrence by catchment based on the UMNR fish distribution dataset compiled for Chapter 2, with catchments delineated by aggregating U.S. Geological Survey hydrologic units (Simley & Carswell, 2009).

The second binary response variable *Spreader* represented invasion success during the spread stage. To investigate traits of spreaders irrespective of native/introduced status, we

analyzed the species pool identified in Chapter 2 of this thesis comprising 74 native and introduced UMNR stream fishes. We distinguished spreaders and nonspreaders based on the Chapter 2 analysis of temporal trends in catch per unit effort (CPUE) in the UMNR since 1938, where CPUE was defined as the number of subwatersheds (U.S. Geological Survey's 6th-level hydrologic units [HUC12s]; Simley & Carswell, 2009) a species was detected in per time period divided by the total number of subwatersheds sampled during the time period. CPUE was then regressed over time for ten time periods, and a null model (no trend in CPUE) compared to competing models indicating temporal change (spread or decline) based on Akaike weights (Burnham & Anderson, 2002). In the current study, species that were classified in Chapter 2 as stable or decliners were assigned *Spreader* = 0, and species classified as spreaders in Chapter 2 were assigned *Spreader* = 1.

We used boosted classification trees (BCT) to identify species traits from **P** that contributed to *Colonizer* and *Spreader*. We developed six BCT models, including: (1) *Colonizer* against biological traits; (2) *Colonizer* against ecological traits; (3) *Colonizer* 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, although GAME was the only introduction attribute that applied to models for *Spreader* since the species pool for this response included both native and introduced species. We also plotted individual classification trees to aid in visualizing and interpreting interactions of traits in the BCT models.

BCT combines two machine-learning techniques, decision trees and boosting. Decision tree models explain variation in a response using one or more explanatory variables (in this study, species traits). Taking one explanatory variable at a time, a tree is built by repeatedly splitting the data into two groups, each of which is as homogenous as possible. At each split, the explanatory variable that maximizes the homogeneity of the two resulting groups is chosen (De'ath & Fabricius, 2000). Decision trees are particularly suited to the analysis of complex ecological data because: they can handle a variety of predictor and response variable types (including continuous, ordinal, and categorical variables) with nonlinear relationships, complex interactions, and missing values; they require no distributional assumptions about the variables; they can handle situations in which the number of predictor variables greatly exceeds the number

of observations; and they are simple to understand and interpret (individual trees can be visualized) (Breiman *et al.*, 1984; De'ath & Fabricius, 2000). For example, decision trees outperformed traditional parametric classification techniques (multiple logistic regression and discriminant function analysis) used to model fish distribution (Olden & Jackson, 2002).

The structure of an individual decision tree is highly dependent on the sample of data. Therefore, the accuracy and stability of decision tree models can be improved using ensemble methods that combine many (100s–1000s) individual trees into a single strong model that is much more accurate than any one of the individual trees (Schapire, 2003). "Boosting" is an ensemble technique that produces a series of decision trees using a learning algorithm that attempts to add new trees to the ensemble that are better able to predict observations for which the previous ensemble's performance was poor. The final BCT model is a linear combination of many trees that can be thought of as a regression model where each term is a tree (Elith, Leathwick & Hastie, 2008).

We computed BCT models for *Colonizer* and *Spreader* with R statistical software (R Core Team, 2014) using the dismo package (Hijmans *et al.*, 2015). We used the gbm.step function to identify the optimal number of trees while systematically changing tree complexity (maximum number of splits per tree) and learning rate (determines the contribution of each tree to the growing model) to minimize predictive deviance and maximize area under the receiver operating characteristic curve (AUC) from 10-fold cross validation (Elith *et al.*, 2008; Table 3.1). BCT models were initially tuned using all traits in the given set (i.e., biological, ecological, or combined) and introduction attributes. Final models were simplified for optimal performance using the gbm.simplify function to drop non-informative or redundant traits. 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, 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, we used the rpart (Therneau, Atkinson & Ripley, 2014) and rpart.plot (Milborrow, 2015) packages to plot an individual classification tree for each model to aid in interpreting trait interactions.

Results

BCT models for *Colonizer* and *Spreader* performed equivalently in terms of AUC scores (Table 3.1). Models using biological traits had higher AUC scores than those based on ecological traits. Models with ecological and biological traits combined performed no better than models based on biological traits.

Traits of colonizers

Biological traits–Twelve biological traits and one introduction attribute (FIRSTREC) were retained in the final BCT model for *Colonizer* (Table 3.2). Partial dependence plots for the four most influential traits (Fig. 3.5a) indicated that strong colonizers were introduced earlier (FIRSTREC), had smaller eyes relative to body length (RELEYEDIA), provided more parental care (PC), or were less opportunistic in their life history (OPPORT_D) than weak colonizers. All 12 species introduced before 1940 were classified as strong colonizers, whereas all five species introduced after 1985 were weak colonizers. The pruned decision tree for *Colonizer* against biological traits (Fig. 3.6a) showed that 10 of 12 weak colonizers (along with 5 of 27 strong colonizers) exhibited a combination of low PC and high RELEYEDIA, but FIRSTREC did not appear in this individual tree. Human preference traits indicating game/non-game status (GAME) and propagule pressure (INTROEFF), along with both physiology traits (TMIN_JAN and TMAX_JUL), were dropped from the *Colonizer* model as non-informative.

Ecological traits–Nine ecological traits and two introduction attributes remained in the final BCT model for *Colonizer* (Table 3.2). Partial dependence plots for the three most influential traits (Fig. 3.5c) indicated that strong colonists tended to be introduced before 1940 (FIRSTREC), the latitude of their native range centroid (LATCEN) was ≥36 degrees N, or the minimum latitude (southern limit) of their native range (LATMIN) was >27 degrees N. The pruned decision tree for *Colonizer* against ecological traits (Fig. 3.6c) showed that 25 of 27 strong colonizers (along with 6 of 12 weak colonizers) were either first detected prior to 1940, or had LATCEN ≥36 degrees N. Four of the five (all except FIRSTREC) most influential ecological traits in the BCT for *Colonizer* were in the geographic distribution domain.

Traits of spreaders

Biological traits–Three biological traits remained in the final BCT model for *Spreader* (Table 3.2). Partial dependence plots (Fig. 3.5b) indicated that spreaders tended to be adapted to warmer winters (TMIN_JAN), or were equilibrium W&R strategists as indicated by smaller EQUIL_D and body length at onset of maturity (LEN1REPRO). A decision tree for *Spreader* against biological traits (Fig. 3.6b) showed that 34 of 43 nonspreaders (along with 7 of 31 spreaders) exhibited a combination of high EQUIL_D and low TMIN_JAN.

To allow further interpretation of the effect of individual life history traits on *Spreader*, the BCT and individual classification tree analyses were repeated with multivariate life history traits EQUIL_D, OPPORT_D, and PERIOD_D excluded. The repeated BCT model for *Spreader* approached the accuracy of the original model (cross-validation AUC = 0.743, SE=0.051) and suggested that the importance of EQUIL_D was mediated by a shorter spawning season (SEASON) and greater PC (Table 3.2, Fig. 3.7a), with possible interactions between TMIN_JAN, LEN1REPRO, and SEASON (Fig. 3.7b).

Ecological traits–Ten ecological traits remained in the final BCT model for *Spreader* (Table 3.2). Partial dependence plots for the five most influential traits (Fig. 3.5d) indicated that spreaders tended to have LATCEN <37 degrees N, native range area (AREAKM2) $<1.4 \times 10^6$ km^2, LATMIN >35 degrees N, longitude of their native range centroid (LONCEN) ≤79 degrees W, or avoided eating algae or phytoplankton (ALGPHYTO). The pruned decision tree for *Spreader* against ecological traits (Fig. 3.6d) showed that 42 of 43 nonspreaders (along with 14 of 31 spreaders) either had AREAKM2 $\geq 1.4 \times 10^6$ km^2, or their native range centroid was located north of 37 degrees N or west of 79 degrees W. As was the case for the *Colonizer* response, four of the five most influential ecological traits for *Spreader* described species' geographic distribution. LATMIN was positively related to both *Colonizer* and *Spreader*; however, LATCEN, AREAKM2, and LONCEN had opposing effects on the two responses.

Discussion

Defining invasion success by stage

Several prior studies have examined species traits of fishes influencing the transport and colonization stages by comparing species introduced to a recipient region (typically a state or

continent) to a pool of unintroduced species from some donor region (Colautti, 2005; Duggan, Rixon & MacIsaac, 2006; Jeschke & Strayer, 2006). Such studies are underrepresented in the literature presumably due to uncertainty over whether introduction of a species has been attempted (failed introductions often go unrecorded) (García-Berthou, 2007) and questions about how to specify the donor region and which non-introduced species to include (Vermeij, 1996). Our solution was to compare strong versus weak colonizers in the recipient region based on the number of UMNR catchments having restricted interconnectivity that were colonized by a species. This approach reflects a species' success in being independently transported into multiple UMNR catchments (transport stage), as well as its ability to survive abiotic filters of the UMNR after release (colonization stage). Our approach avoids the need to identify a donor region and non-introduced biota, but does not alleviate potential bias due to unrecorded failed introductions. And since an unknown number of introductions may remain undetected until after the colonization stage, our *Colonizer* response as defined may also represent species traits associated with the establishment or early spread phases of invasion.

Measures of success during the spread stage in prior studies of species traits of invasive fishes have included the number of invaded catchments irrespective of time since introduction (Marchetti *et al.*, 2004; Ribeiro *et al.*, 2008), number of lakes invaded per year since introduction (Kolar & Lodge, 2002), and change in river length occupied over a time interval (Vila-Gispert *et al.*, 2005). The species pool considered in each of the aforementioned studies comprised only introduced fishes. Our approach differed in two ways: (1) To investigate traits of spreaders irrespective of their native/introduced status (i.e., including native invaders), we analyzed a species pool comprising both native and non-native tributary fishes of the UMNR. (2) We took a CPUE-based statistical approach to classify spreaders versus nonspreaders that accounted for the effect of temporal variation in sampling effort (see Chapter 2).

Colonizer traits

The year an introduced species was first detected in the New River drainage (FIRSTREC) was the most influential predictor of colonization success for both the biological and ecological traits models. Introduced species first detected before approximately 1940 had the highest probability of eventually colonizing all three UMNR catchments. One explanation is that the two dams and reservoirs isolating the three UMNR catchments were constructed in 1934

(Little River Dam) and 1939 (Claytor Dam); thus, greater connectivity of the three catchments prior to 1939 may have facilitated a "strong colonizer" status for early introductions. The *Colonizer* partial dependence plots (Fig. 3.5a,b) show a second drop in colonization success around 1980. This 1980 threshold may be explained by a lag between initial release and subsequent detection, or may be related to tapering of state-sponsored stocking of new gamefish species after the 1970s (Jenkins & Burkhead, 1994).

Although we found no other study that included time (since introduction) among the candidate predictors for colonization success, time was positively associated with invasion success in later stages of freshwater fish invasions in two studies (Ruesink, 2005; Vila-Gispert *et al.*, 2005). The role of time in establishment of birds and plants was equivocal (Kolar & Lodge, 2001). Our results reinforce that time since introduction (or at least detection) should be included in statistical analyses of invasion success (García-Berthou, 2007; Barney & Whitlow, 2008; Catford *et al.*, 2009) for any stages after transport and release (time-zero), not because time itself affects invasion outcomes (it cannot), but because the nature of an invasion and its drivers (e.g., propagule pressure) vary through time (Catford *et al.*, 2009; Fig. 3.1).

Strong colonizers were associated with a suite of biological traits related to benthic feeding, including smaller relative eye diameter (RELEYEDIA) and a more bottom-oriented mouth position (MTHPOS) and angle (MTHANG). Positive correlation of RELEYEDIA with MTHPOS (Pearson's $r = 0.376$, $p = 0.001$) and MTHANG ($r = 0.351$, $p = 0.002$) for UMNR species suggests these traits may be linked to a coevolved benthic feeding strategy (Frimpong & Angermeier, 2010). One explanation for the contribution of benthic feeding traits to colonization success could be that humans (e.g., live-bait fishermen) preferentially selected benthic species for transport into the UMNR. However, the non-significance of human-preference traits (GAME & INTROEFF) in our BCT model for *Colonizer* undermines this explanation. Selection favoring benthic feeders during the colonization through early establishment stages (i.e., survival of released individuals and population increase to detectable levels) is a more plausible, though untested hypothesis. The strong negative effect of RELEYEDIA on *Colonizer* suggests a mechanism involving selection against highly visual feeders, e.g., perhaps due to increased suspended sediments resulting from 19th–20th century land use activities (deforestation, agriculture, residential development). The interaction between RELEYEDIA and parental care

(PC) depicted in the pruned decision tree for *Colonizer* against biological traits (Fig. 3.6a) suggests that RELEYEDIA was especially important for species that provided less PC.

Another pair of ethologically linked biological traits contributing to *Colonizer* included parental care (PC) and distance in W&R traits space to the opportunistic end-point (OPPORT_D). Species with increased colonization success were farther from the opportunistic end-point (making them either equilibrium or periodic strategists) and provided more parental care. This combination of traits describes an equilibrium W&R life history strategy (Fig. 3.3). By emphasizing juvenile survival over egg production, equilibrium strategists are better adapted to environments having stable, predictable conditions and mortality factors, where ecological filters are dominated more by biotic interactions and less by unpredictable abiotic disturbances (Winemiller & Rose, 1992).

By reducing flow variation, dams create a more stable environment that favors equilibrium species (Olden *et al.,* 2006; Mims & Olden, 2013; McManamay & Frimpong, 2015). The 2005 National Inventory of Dams (NID; USACE, 2005) listed 69 dams >2 m in height in the UMNR. Version 931v210 of the high-resolution (1:24,000-scale) National Hydrography Dataset (NHD; Simley & Carswell, 2009) included 1,602 "LakePond" or "Reservoir" waterbodies that intersected an NHD flowline (i.e., a stream) in the UMNR, only one of which (Mountain Lake) was a natural waterbody (Jenkins & Burkhead, 1994). Despite their large number, the total surface area of these NHD waterbodies, including the 18 km^2 Claytor Lake, covered just 26 km^2, which represented 0.27% of the 9,700 km^2 UMNR (<0.1% not counting Claytor Lake). Thus, it seems unlikely that the effect of flow regulation alone fully explains the enhanced colonization success observed for equilibrium species in the UMNR.

PC was the second-most important biological trait explaining colonization success. Juvenile survival, mediated by PC, is a key defining trait of the equilibrium life-history strategy. Therefore, perhaps the success of equilibrium strategists in the UMNR was driven mainly by selective advantages afforded by higher PC. Sixteen of the 17 introduced species having PC ≥0.39 were classified as strong colonizers (Fig. 3.6a). All 16 of these strong colonizers participate in nest spawning, either by building their own nests (14 species), or by habitually spawning in the nest of another species (nest associates, two species). Nesting behavior can enhance reproductive success in highly silted streams by providing unsilted substrate needed for survival of developing embryos (Peoples, Tainer & Frimpong, 2011; Peoples, Blanc &

69

Frimpong, 2015). Nest builders also frequently guard the nest against egg predators or bury eggs for the same effect (Jenkins & Burkhead, 1994). Nest association is considered to be a mutualistic interaction, as the host also benefits from reduced predation on its own eggs through a dilution effect (Johnston, 1994; Peoples & Frimpong, 2013). If *Colonizer* represented colonization success during the transport and colonization stages, we would not expect to see a strictly reproductive trait such as PC among its most important predictors. This may indicate some influence on our *Colonizer* response from ecological filters acting on the establishment stage, perhaps attributable to a lag between colonization and initial detection.

Ecological traits that contributed most to colonization success included FIRSTREC (discussed above) and a suite of traits describing the geographic distribution of a species' native range: LATCEN; LATMIN; and AREAKM2. All except FIRSTREC were positively associated with *Colonizer*. Latitude and range size are related to physiological tolerance (e.g., temperature limits and breadth of tolerance, respectively) (Theoharides & Dukes, 2007; Frimpong & Angermeier, 2009). Thus, the important ecological traits in our BCT model seem to indicate a colonization advantage for species introduced from cooler northern latitudes, and species having a broader temperature tolerance range. Perhaps northern species released into UMNR waters are better matched to the highland climate (especially colder winters) and montane aspect of the UMNR, facilitating their survival through the colonization stage. In general, widespread species are also more likely to come into human contact and therefore be transported. The effect of LATMIN likely reflects intolerance of subtropical species to the UMNR's colder winters.

However, we interpret our findings for the BCT *Colonizer* model against ecological traits with caution, because the accuracy of this model in discriminating strong and weak colonizers was poor (AUC = 0.66 from cross-validation). The model using biological traits was more accurate (AUC = 0.79), and should therefore better explain colonization. Also, ecological traits are indirect expressions of biological traits; therefore, biological traits, if properly selected and accurately measured, are expected to better explain observed ecological processes and be more amenable to mechanistic interpretation of those processes (Frimpong & Angermeier, 2010). All three biological traits expected to more accurately represent physiological effects were dropped as non-informative from the BCT model for *Colonizer*. These included average air temperature minimum at the native range centroid for January (TMIN_JAN) and the maximum for July (TMAX_JUL), and minimum spawning temperature (TSPAWNMIN). The analysis using

70

biological traits indicates greater support for the contribution of feeding morphology and life history traits for this pool of species, rather than physiology/climate tolerance traits, to colonization success.

Spreader traits

UMNR spreaders were most strongly associated with warmer winters (TMIN_JAN). Air temperature in the New River basin has warmed by 0.4–0.6 C over the past 40 years (Huang & Frimpong, 2016), and air-water temperature relationships are typically strong (Erickson & Stefan, 2000). However, heat is added to streams through many human influences including (but not limited to) riparian deforestation, water storage behind dams, increased stream channel width/depth ratio through streambank erosion, water withdrawal and wastewater discharge, and stormwater runoff (Poole & Berman, 2001). Thus, through various land-use practices, especially riparian deforestation, humans have likely increased water temperature in the UMNR's naturally cool–cold highland streams, thereby facilitating invasions by warmwater species (Angermeier & Winston, 1998; Jones *et al.*, 1999; Scott & Helfman, 2001).

UMNR spreaders were also associated with an equilibrium life history, as indicated by low values of EQUIL_D, which appeared to be mediated by a shorter spawning season and higher parental care. As discussed in the previous section, the strong contribution of equilibrium traits suggests that spreaders have benefited from more stable, or perhaps more stressful, environmental conditions in the UMNR since the 1930s. Flow regulation (dams) in the UMNR might have benefited native and introduced equilibrium strategists by creating a more stable abiotic environment in which trade-offs between reproductive effort and juvenile survival are more likely to pay off (Winemiller, 2005). However, the <1% cover of impoundments in the UMNR suggests that UMNR tributaries are minimally regulated.

Habitat alteration has likely played a larger role than flow regulation in selecting for equilibrium spreaders in UMNR tributaries. Particularly in montane streams which are dominated by rocky substrate, many fish and prey organisms utilize spaces under and between rocks not just for protection of developing embryos in gravel nests (as discussed above), but also for protection from swift water and for concealment from predators and prey. Riparian deforestation leads to filling of riffles and shallow pools with fine sediments, thereby reducing habitat diversity (Jones et al., 1999; Scott & Helfman, 2001), and perhaps making unfilled

cavities a limiting resource subject to increased competition. Due to their greater emphasis on survival relative to reproduction, species possessing equilibrium traits are expected to have higher fitness under conditions of chronic competition or stress (Winemiller, 2005). Thus, equilibrium traits such as a brief spawning season and greater parental care may be advantageous under increased competition for microhabitat types in a degraded environment.

Geographic distribution traits LATCEN, AREAKM2, and LATMIN contributed heavily to the BCT model for *Spreader*, as was also the case for *Colonizer*. However, LATCEN and AREAKM2 had opposing effects on *Colonizer* and *Spreader*. Colonization increased with LATCEN, but spread decreased. And species with the smallest AREAKM2 showed increased spread but decreased colonization. While keeping in mind the caveat about poor performance of ecological traits discussed in the preceding section, the opposing effects of geographic distribution traits on *Colonizer* and *Spreader* may reflect a transition in dominant ecological filters between stages (Fig. 3.1; Vermeij, 1996; Kolar & Lodge, 2001; Marchetti *et al.*, 2004; Theoharides & Dukes, 2007). Traits that help founders survive (e.g. climate match, tolerance) are essential to overcome abiotic filters during the colonization stage (Theoharides & Dukes, 2007). Thus, the positive effect of LATCEN on *Colonizer* may reflect climate matching in a highland receiving environment. However, in the post-colonization stages, biotic interactions and landscape filters take on an increasing role as small, isolated founding colonies adapt to the receiving environment and integrate into the biotic community (Sakai *et al.*, 2001), and disperse away from introduction sites. The negative effect of LATCEN on *Spreader* might demonstrate the ability of southern species to occupy novel warmwater niche space created by widespread human land-use practices across the UMNR landscape (Angermeier & Winston, 1998; Scott & Helfman, 2001; Lapointe *et al.*, 2012). Likewise, the modeled effect of AREAKM2 on *Colonizer* may reflect advantages during the transport stage of large range size resulting in greater human contact. And one can imagine plausible advantages associated with reduced range size (e.g., montane-adapted species have smaller range size) and an eastern distribution (e.g., Atlantic-slope lowland species adapted to novel warmwater niches) that might be beneficial in the UMNR during the establishment and spread stages. The modeled tendency of successful spreaders to avoid algae or phytoplankton in the diet (ALGPHYTO) may be explained by release from competition for a limited food resource. The three most abundant and widespread (and still spreading; see Chapter 2) UMNR species, central stoneroller *Campostoma anomalum*, mountain

72

redbelly dace *Chrosomus oreas*, and bluehead chub *Nocomis leptocephalus* are all avid algae eaters (Jenkins & Burkhead, 1994).

Biological versus ecological traits

The use of biological traits combined with introduction attributes enhanced the accuracy of models of invasion outcomes for New River stream fishes, whereas ecological traits had less predictive ability. Biological traits are also expected to be more amenable to mechanistic interpretation than ecological traits (Poff *et al.*, 2006; Vieira *et al.*, 2006; Frimpong & Angermeier, 2010). We expect these advantages of biological traits to be generally applicable across taxa and regions. These findings underscore the value of basic research on the physiological, morphological, reproductive, and life-history traits of species, the need for which is demonstrated by a lack of published data on fundamental biological traits such as egg diameter, larval length, and thermal tolerance for many species in this study. Although the phylogenetic signal must be accounted for before making inter-specific comparisons involving biological traits, techniques such as phylogenetically independent contrasts (Felsenstein, 1985), phylogenetic generalized least squares (Grafen, 1989), and phylogenetic eigenvector regression (Diniz-Filho *et al.*, 1998) are available to researchers.

Conclusions

Do strong colonizers and spreaders share traits that consistently differentiate them from weak colonizers and nonspreaders?

Yes. Models using biological traits accurately explained colonization and spread success in the UMNR. Time since introduction, a benthic-feeding strategy, an equilibrium life history strategy, and parental care in the form of nest spawning predicted colonization success. Temperature tolerance (warmer winters) and equilibrium life history predicted successful spreaders. Models using ecological traits demonstrated some plausible relationships with invasion success, but their interpretability was limited by low accuracy and indirect linkages to biological mechanisms.

Do influential species traits differ between colonization and spread stages?

Although the species pools differed in our models of colonization (non-native species only) and spread (both native and non-native species), an equilibrium life-history strategy was associated with both successful colonizers and spreaders. Other biological traits differed, possibly indicating a shift in dominant ecological filters between invasion stages.

How important are introduction attributes (propagule pressure, time since introduction, game/non-game status) compared to biological and ecological species traits in influencing invasion outcomes?

Time since introduction was the most important predictor of colonization success in the biological traits model and the ecological traits model. Variables that estimated human use (GAME) and propagule pressure (INTROEFF) were non-informative. It is doubtful that these human-preference attributes are truly unimportant in driving invasion outcomes. Rather, our estimates of these values may have been too imprecise (García-Berthou, 2007).

What can we infer using a traits-based approach about dominant ecological filters shaping the New River fish assemblage?

Influential biological and ecological traits in our models for colonization and spread support the hypothesis that anthropogenic disturbance has increased the invasibility of UMNR tributaries. Successful invaders possessed traits expected to enhance performance in warmer water, reduced water clarity, silt-embedded substrates, and conditions of chronic stress. Specific traits associated with increased invasion success highlight opportunities to strategically restore natural processes (e.g., reforest riparian zones, exclude cattle from streams, restore riparian wetlands, stabilize failing stream banks) in selected UMNR watersheds to bolster environmental resistance to invasions. A follow-up study on the spatial distribution of highly and minimally invaded UMNR subwatersheds and land-use variables contributing to invasibility is needed to confirm inferences from the present study and guide efficient allocation of research and restoration efforts.

Acknowledgments

Carolina Dept. of Environment & Natural Resources' Stream Fish Community Assessment Program) for their thorough responses to our introduction-effort survey; and J. Huang and B. Peoples for helpful discussions.

References

Alcaraz C., Vila-Gispert A. & García-Berthou E. (2005) Profiling invasive fish species: the importance of phylogeny and human use. *Diversity and Distributions*, **11**, 289–298.

Angermeier P.L. & Winston M.R. (1998) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**, 911–927.

Balon E.K. (1975) Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada*, **32**, 821–864.

Barney J.N. & Whitlow T.H. (2008) A unifying framework for biological invasions: the state factor model. *Biological Invasions*, **10**, 259–272.

Betancur R., Broughton R.E., Wiley E.O., Carpenter K., López J.A., Li C., *et al.* (2013) The tree of life and a new classification of bony fishes. *PLOS Currents Tree of Life*, edition 1. Available: http://currents.plos.org/treeoflife/article/the-tree-of-life-and-a-new-classification-of-bony-fishes/ (February 2015).

Blackburn T.M., Pysek P., Bacher S., Carlton J.T., Duncan R.P., Jarosik V. *et al.* (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, **26**, 333–339.

Breiman L., Friedman J.H., Olshen R.A. & Stone C.J. (1984) *Classification and regression trees*. Wadsworth International Group, Belmont, CA.

Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd edition. Springer-Verlag, New York.

Campbell M.A., López J.A., Sado T. & Miya M. (2013) Pike and salmon as sister taxa: Detailed intraclade resolution and divergence time estimation of Esociformes + Salmoniformes based on whole mitochondrial genome sequences. *Gene*, **530**, 57–65.

Catford J.A., Jansson R. & Nilsson C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions,* **15**, 22–40.

Clavero M. & García-Berthou E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, **20**, 110.

Colautti R.I. (2005) Are characteristics of introduced salmonid fishes biased by propagule pressure? *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 950–959.

Cypriniformes Commons (2012) *Cypriniformes Tree of Life*, beta tree 0912. Available: http://cypriniformes.org/CToL-beta-tree-0912.html (February 2015).

De'ath G. & Fabricius K.E. (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*, **81**, 3178–3192.

Diniz-Filho J.A.F., Ramos de Sant'Ana C.E., & Bini L.M. (1998) An eigenvector method for estimating phylogenetic inertia. *Evolution*, **52**, 1247–1262.

Drake J.A., Mooney H.A., Di Castri F., Groves F., Kruger F.J., Rejmanek M. *et al.* (1989) *Biological Invasions: a Global Perspective*. John Wiley and Sons, New York.

Duggan I.C., Rixon C.A.M. & MacIsaac H.J. (2006) Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. *Biological Invasions*, **8**, 377–382.

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

Erickson T.R. & Stefan H.G. (2000) Linear air/water temperature correlations for streams during open water periods. *Journal of Hydrologic Engineering*, **5**, 317–321.

Felsenstein J. (1985) Phylogenies and the comparative method. *The American Naturalist*, **125**, 1–15.

Fisher D.O. & Owens I.P.F. (2004) The comparative method in conservation biology. *Trends in Ecology and Evolution*, **19**, 391–398.

Friedman J.H. (2001) Greedy function approximation: a gradient boosting machine. *Annals of Statistics*, **29**, 1189–1232.

Frimpong E.A. & Angermeier P.L. (2009) Fish traits: a database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries*, **34**, 487–495.

Frimpong E.A. & Angermeier P.L. (2010) Trait-based approaches in the analysis of stream fish communities. *American Fisheries Society Symposium*, **73**, 109–136.

Froese R. & Binohlan C. (2000) Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology,* **56,** 758-773.

Froese R. & Pauly D, editors (2015) *FishBase.* www.fishbase.org (November 2015).

Frontier S. (1976). Decrease of eigenvalues in principal component analysis-comparison with broken stick model. *Journal of Experimental Marine Biology and Ecology*, **25**, 67–75.

Fry J., Xian G., Jin S., Dewitz J., Homer C., Yang L. *et al.* (2011) Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing*, **77**, 858-864.

García-Berthou E. (2007) The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology*, **71** (Supplement D), 33–55.

Gido, K.B & Brown J.H. (1999) Invasion of North American drainages by alien fish species. *Freshwater Biology*, **42**, 387–399.

Gower J.C. (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **53**, 325–338.

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society of London*. Series B, Biological Sciences:119–157.

Grinnell, J. (1919) The English house sparrow has arrived in Death Valley: an experiment in Nature. *The American Naturalist*, **53**, 468–472.

Hardman M. (2005) The phylogenetic relationships among non-diplomystid catfishes as inferred from mitochondrial cytochrome *b* sequences; the search for the ictalurid sister taxon (Otophysi: Siluriformes). *Molecular Phylogenetics and Evolution*, **37**, 700–720.

Helfman, G. S. (2007). Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources. Island Press, Washington D.C.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978. GIS data available: worldclim.org (October 2015).

Hijmans R.J., Phillips S., Leathwick J. & Elith J. (2015) *dismo: Species Distribution Modeling*. R package version 1.0-12. http://CRAN.R-project.org/package=dismo

Huang J. & Frimpong E.A. (2016) Temporal transferability of stream fish distribution models: can uncalibrated SDMs predict distribution shifts over time? *Diversity and Distributions* (in press).

Jenkins R.E. & Burkhead N.M. (1994) *Freshwater Fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.

Jeschke J.M. & Strayer D.L. (2006) Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology*, **12**, 1608–1619.

Johnston C.E. (1994) Nest association in fishes: evidence for mutualism. *Behavioral Ecology and Sociobiology*, **35**, 379–383.

Jones E.B.D. III, Helfman G.S., Harper J.O. & Bolstad P.V. (1999) Effects of riparian forest removal on fish assemblages in southern Appalachian streams. *Conservation Biology*, **13**, 1454–1465.

Kolar C.S. & Lodge D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.

Kolar C.S. & Lodge D.M. (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science*, **5596**, 1233–1235.

Lapointe N.W.R, Thorson J.T. & Angermeier P.L. (2012) Relative roles of natural and anthropogenic drivers of watershed invasibility in riverine ecosystems. *Biological Invasions*, **14**, 1931–1945.

Lavoué S., Miya M., Musikasinthorn P., Chen W. & Nishida M. (2013) Mitogenomic evidence for an Indo-West pacific origin of the Clupeoidei (Teleostei: Clupeiformes). *PLoS ONE*, **8**(2): e56485.

Lockwood J.L., Cassey P. & Blackburn T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

López J.A., Chen W.J. & Ortí G. (2004) Esociform phylogeny. *Copeia*, **2004**, 449–464.

Lorion C.M. & Kennedy B.P. (2009) Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. *Ecological Applications*, **19**, 468–479.

Marchetti M.P., Moyle P.B. & Levine R. (2004). Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology*, **49**, 646-661.

McManamay R.A. & Frimpong E.A. (2015) Hydrologic filtering of fish life history strategies across the US: Implications of streamflow alteration on fish assemblages. *Ecological Applications*, **25**, 243–263.

Milborrow, S. (2015). *rpart.plot: Plot rpart Models. An Enhanced Version of plot.rpart*. R package version 1.5.2. http://CRAN.R-project.org/package=rpart.plot

Miller R.R., Williams J.D. & Williams J.E. (1989) Extinctions of North American fishes during the past century. *Fisheries*, **14**, 22–38.

Mims M.C. & Olden J.D. (2013) Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology*, **58**, 50–62.

Olden J.D. & Jackson D.A. (2002) A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biology*, **47**, 1976–1995.

Olden J.D., Poff N.L. & Bestgen K.R. (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs*, **76**, 25–40.

Olden J.D., Poff N.L. & Bestgen K.R. (2008) Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology*, **89**, 847–856.

Omernik J.M. (1987) Ecoregions of the conterminous United States. *Annals of the Association of American Geographers,* **77**, 118–125.

Page L.M. & Burr B.M. (2011) *Peterson Field Guide to Freshwater Fishes of North America North of Mexico*, 2nd edition. Houghton Mifflin Harcourt, New York, NY.

Pendleton R.M., Pritt J.J., Peoples B.K. & Frimpong E.A. (2012) The strength of *Nocomis* nest association contributes to patterns of rarity and commonness among New River, Virginia cyprinids. *American Midland Naturalist*, **168**, 202-212.

Peoples B.K., Blanc L.A. & Frimpong E.A. (2015) Lotic cyprinid communities can be structured as nest webs and predicted by the stress-gradient hypothesis. *Journal of Animal Ecology*, **84**, 1666–1677.

Peoples B.K. & Frimpong E.A. (2013) Evidence of mutual benefits of nest association among freshwater cyprinids and implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **23**, 911–923.

Peoples B.K., Tainer M.B. & Frimpong E.A. (2011) Bluehead chub nesting activity: a potential mechanism of population persistence in degraded stream habitats. *Environmental Biology of Fishes*, **90**, 379–391.

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M. *et al.* (2011) Niches and geographic distributions. Chapter 3 In: *Ecological Niches and Geographic Distributions. Monographs in Population Biology*, **49**. Princeton University Press, Princeton, New Jersey.

Pianka E.R. (1970) On *r*- and *K*-selection. The American Naturalist, **104**, 592–597.

Pimentel D., Zuniga R. & Morrison D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.

Poff N.L., Olden J.D., Vieira N.K.M, Finn D.S., Simmons M.P., & Kondratieff B.C. (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, **25**, 730–755.

Poole G.C. & Berman C.H. (2001) An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental Management*, **27**, 787–802.

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org/.

Ribeiro F., Elvira B., Collares-Pereira M.J. & Moyle P.B. (2008) Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biological Invasions*, **10**, 89–102.

Richardson D.M., Pysek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Roe K.J., Harris P.M. & Mayden R.L. (2002) Phylogenetic relationships of the genera of North American sunfishes and basses (Percoidei: Centrarchidae) as evidenced by the mitochondrial cytochrome *b* gene. *Copeia*, **2002**, 897–905.

Rosebery D.A. (1951) Fishery management of Claytor Lake, an impoundment on the New River in Virginia. *Transactions of the American Fisheries Society*, **80**, 194-209.

Ruesink J.L. (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology*, **19**, 1883–1893.

Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A. *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology, Evolution, and Systematics*, **32**, 305–332.

Sax D.F., Stachowicz J.J., Brown J.H., Bruno J.F., Dawson M.N., Gaines S.D. *et al.* (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution*, **22**, 465–471.

Schapire R.E. (2003) The boosting approach to machine learning: an overview. Chapter 8 *In*: Denison D.D., Hansen M.H., Holmes C.C., Mallick B. & Yu B., editors. *Nonlinear Estimation and Classification*. Springer-Verlag, New York.

Scott M.C. & Helfman G.S. (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, **26**, 6–15.

Scott J. & Panetta F. (1993) Predicting the Australian weed status of southern African plants. *Journal of Biogeography*, **20**, 87–93.

Simley J.D. & Carswell W.J. Jr (2009) The national map–hydrography. *U.S. Geological Survey Fact Sheet 2009-3054*.

Smith W.L. & Busby M.S. (2014) Phylogeny and taxonomy of sculpins, sandfishes, and snailfishes (Perciformes: Cottoidei) with comments on the phylogenetic significance of their early-life-history specializations. *Molecular Phylogenetics and Evolution*, **79**, 332–352.

Smith T.A., Ciccotto P.J., Mendelson T.C. & Page L.M. (2014) Dense taxon sampling using AFLPs leads to greater accuracy in phylogeny estimation and classification of darters (Percidae: Etheostomatinae). *Copeia*, **2014**, 257–268.

Theoharides K.A. & Dukes J.S. (2007) Plant invasions across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256–273.

Therneau T., Atkinson B., & Ripley B. (2014). *rpart: Recursive Partitioning and Regression Trees*. R package version 4.1-8. http://CRAN.R-project.org/package=rpart

USACE (U.S. Army Corps of Engineers) (2005) *2005 National Inventory of Dams*. Available: http://www.fws.gov/r5gomp/gom/cv/dam_nid.htm (June 2015).

Vermeij G.J. (1996) An agenda for invasion biology. *Biological Conservation*, **78**, 3–9.

Vieira N.K.M., Poff N.L., Carlisle D.M., Moulton S.R. II, Koski M.L. & Kondratieff B.C. (2006) *A database of lotic invertebrate traits for North America*. U.S. Geological Survey, Data Series 187, Reston, Virginia.

Vila-Gispert A., Alcaraz C. & García-Berthou E. (2005) Life-history traits of invasive fish in small Mediterranean streams. *Biological Invasions*, **7**, 107–116.

Williamson M. (1996) *Biological Invasions*. Chapman & Hall, London.

Winemiller K.O. (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 872–885.

Winemiller K.O. & Rose K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2196–2218.

Table 3.1 Tuning and performance of boosted classification tree models for the contribution to two binary response variables *Colonizer* and *Spreader* of traits of 39 established introduced and 35 native fish species reported from upper and middle New River tributaries. "Variables dropped" = number of redundant/non-informative explanatory variables (traits) dropped from the final simplified model. "Min. no. obs. in leaf" = minimum number of observations (species) in a terminal node. "CV AUC (SE)" = mean cross-validated area under the receiver operating characteristic curve (followed by standard error).

Response:	*Colonizer* (n = 39 introduced spp.)			*Spreader* (n = 74 introduced & native spp.)		
Traits:	Biological	Ecological	Combined	Biological	Ecological	Combined
Variables dropped	11	10	22	19	9	21
Tree complexity	3	3	3	3	3	3
Learning rate	0.001	0.0005	0.001	0.001	0.0005	0.001
No. of trees	4250	1650	5050	2300	950	3650
Min. no. obs. in leaf	5	5	5	10	10	10
Bag fraction	0.75	0.75	0.75	0.5	0.5	0.5
CV AUC (SE)	0.793 (0.053)	0.66 (0.102)	0.82 (0.064)	0.79 (0.042)	0.648 (0.067)	0.755 (0.032)

Table 3.2 Boosted classification tree analyses of relative influence (%) on *Colonizer* and *Spreader* responses of biological (left) and ecological (right) species traits, and introduction attributes (marked with *) (defined in Table S5) of 39 established introduced and 35 native fish species reported from tributaries of the upper and middle New River. Traits contributing >5% to the response are shown in bold, and their relative influence values are prefixed with + or – to indicate whether the trait had a positive or negative relationship with the response, based on the general trend in the partial dependence plot (Fig. 3.5). Traits are listed in descending order by their maximum relative influence across both responses. A "-" indicates redundant/non-informative traits that were dropped from the final simplified model. Introduction attributes *FIRSTREC* and *INTROEFF* apply only to introduced species, and therefore were excluded from the analysis for *Spreader*, which considers both native and introduced species. The analysis for *Spreader* using biological traits was repeated with multivariate life history traits EQUIL_D, OPPORT_D, and PERIOD_D excluded (shown in column four as NA) to allow further interpretation of the effect of individual life history traits (partial dependence plots for the repeated analysis appear in Fig. 3.7).

Biological trait	Response			Ecological trait	Response	
	Colonizer	*Spreader*			*Colonizer*	*Spreader*
TMIN_JAN	-	**+38.6**	**+33.2**	FIRSTREC*	**-37.2**	NA
EQUIL_D	2.9	**-33.2**	NA	LATCEN	**+25.5**	**-32.8**
LEN1REPRO	3.7	**-28.2**	**-26.2**	AREAKM2	**+7.9**	**-24.6**
FIRSTREC*	**-21.6**	NA	NA	LATMIN	**+14.1**	**+15.0**
SEASON	-	-	**-20.8**	LONCEN	**-5.7**	**+9.8**
RELEYEDIA	**-14.5**	-	-	ALGPHYTO	1.1	**-8.1**
PC	**+13.8**	-	**+19.8**	INTROEFF*	3.9	NA
OPPORT_D	**+8.9**	-	NA	SURWCOL	-	2.6
MTHPOS	**-7.8**	-	-	FSHCRCRB	2.2	-
MTHANG	**-7.2**	-	-	PREFLOT	0.7	2.1
FECUNDITY	**-5.6**	-	-	MONTANE	1.1	1.9
SWMFACT	**-5.3**	-	-	SLOWCURR	-	1.6
SERIAL	4.2	-	-	LOWLAND	-	1.4
PERIOD_D	2.5	-	NA	EGGS	0.6	-
SHPFACT	2.0	-	-	BENTHIC	-	-
AGE1REPRO	-	-	-	CREEK	-	-
GAME*	-	-	-	GAME*	-	-
GENTIME	-	-	-	LARGERIV	-	-
INTROEFF*	-	NA	NA	LITHOPHIL	-	-
LONGEVITY	-	-	-	PHYSIOBRE	-	-
RELMANLEN	-	-	-	WATBRE	-	-
TIMING	-	-	-			
TMAX_JUL	-	-	-			
TSPAWNMIN	-	-	-			
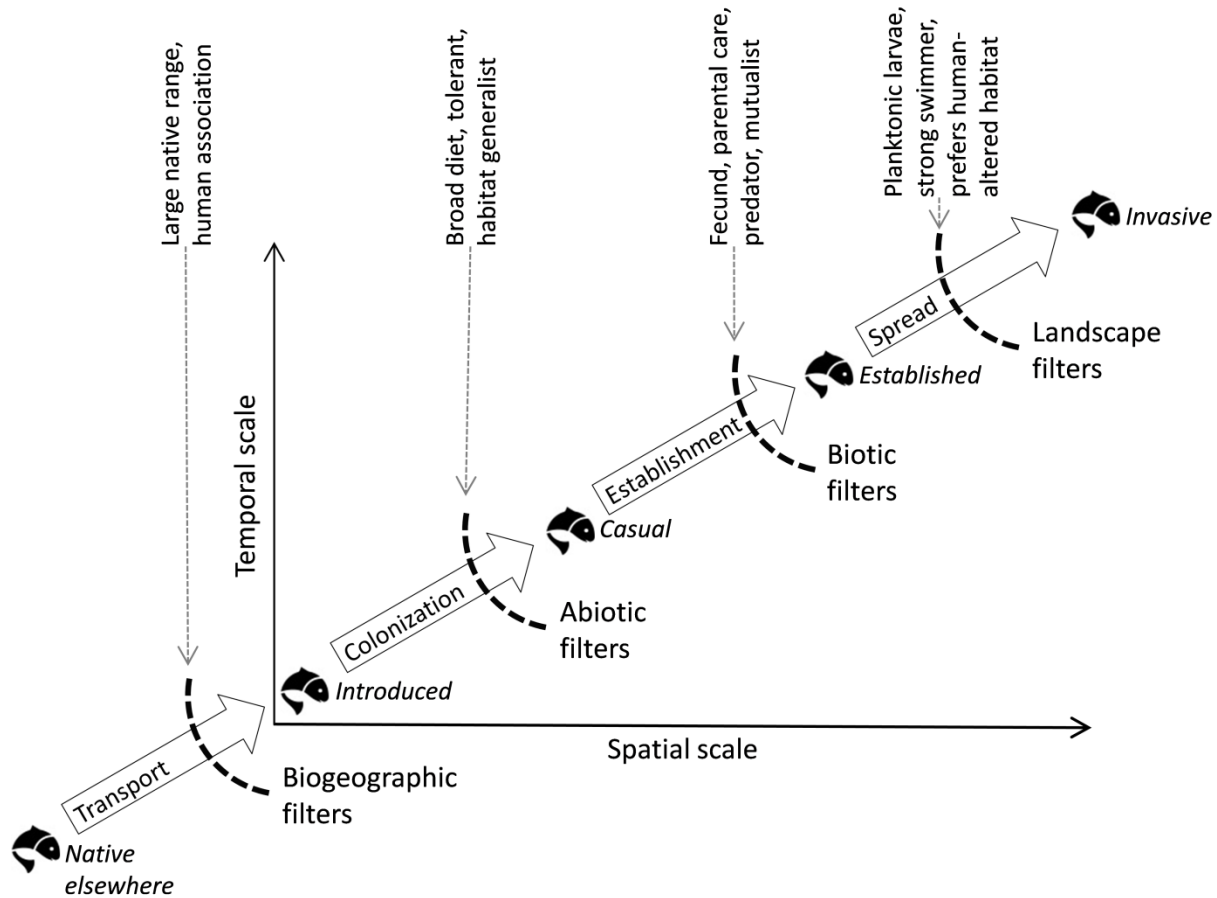
Fig. 3.1 Four-stage invasion model adapted from Theoharides & Dukes (2007). A would-be invader must possess traits (example traits labeled along top of figure) enabling it to surmount the suite of filters/barriers characteristic of each stage. As an invasion progresses through the stages, the temporal and spatial extents of invasion processes generally increase. The transport stage is shown outside the spatial and temporal axes because human-assisted transplants of introduced species can occur much faster, and over larger distances, than most natural movements of species.

Fig. 3.2 The **B**iotic-**A**biotic-**M**ovement-**H**uman (BAM-H) diagram adapted from Peterson *et al.* (2011) and Catford *et al.* (2009) represents distributional areas for a given species, including areas where biotic interactions with other species are favorable (B), abiotic conditions and resources are suitable (A), and that are accessible (M). B∩A∩M defines occupied areas (O). B∩A∩M^c defines invadable areas (I). Humans (H) may modify B, A, or M (and therefore O and I also).
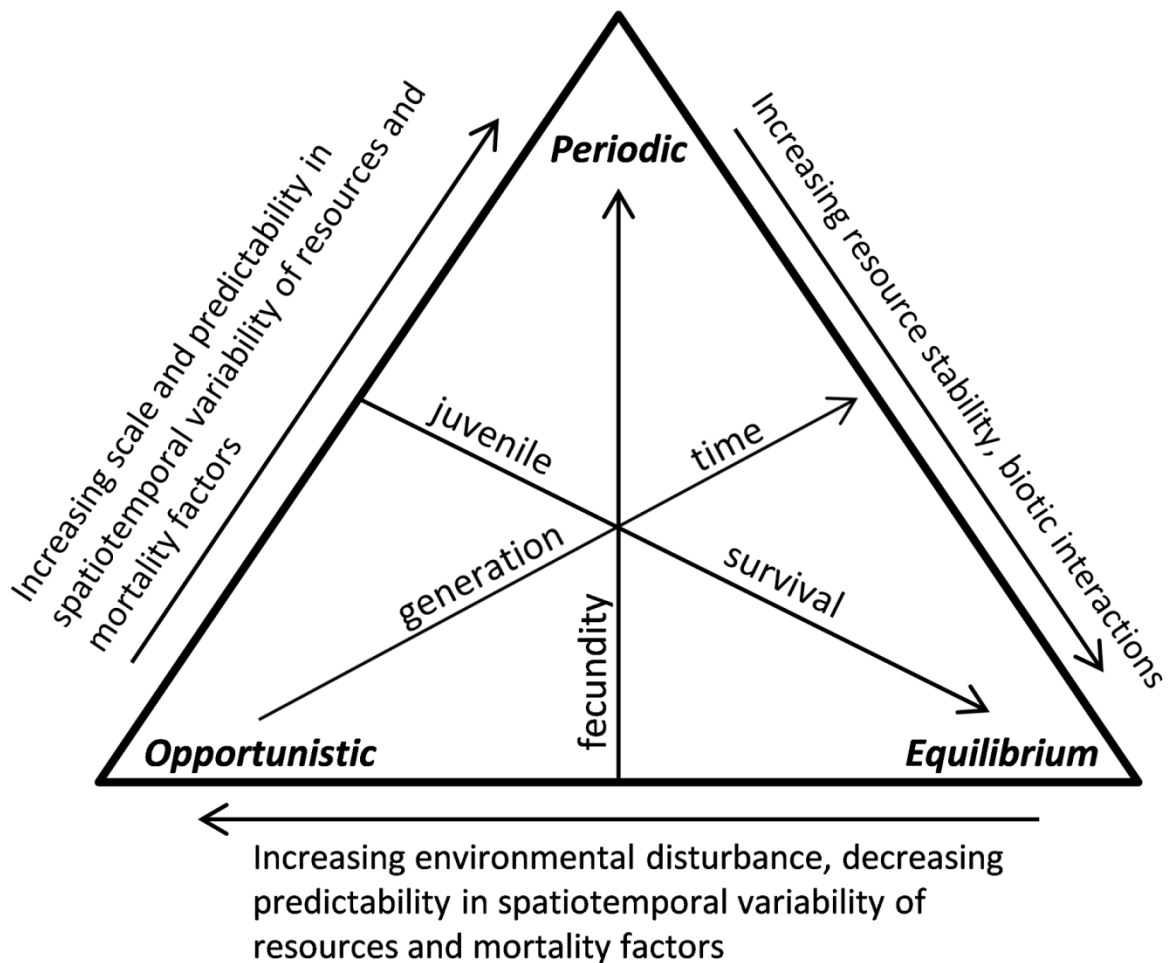
Fig. 3.3 Triangular fish life-history continuum model of Winemiller (2005) originally conceptualized by Winemiller & Rose (1992). Three life-history end-point strategies (periodic, opportunistic, equilibrium) result from trade-offs between fecundity, juvenile survival, and generation time (inside arrows) in response to the predictability and scale of environmental conditions (outside arrows).
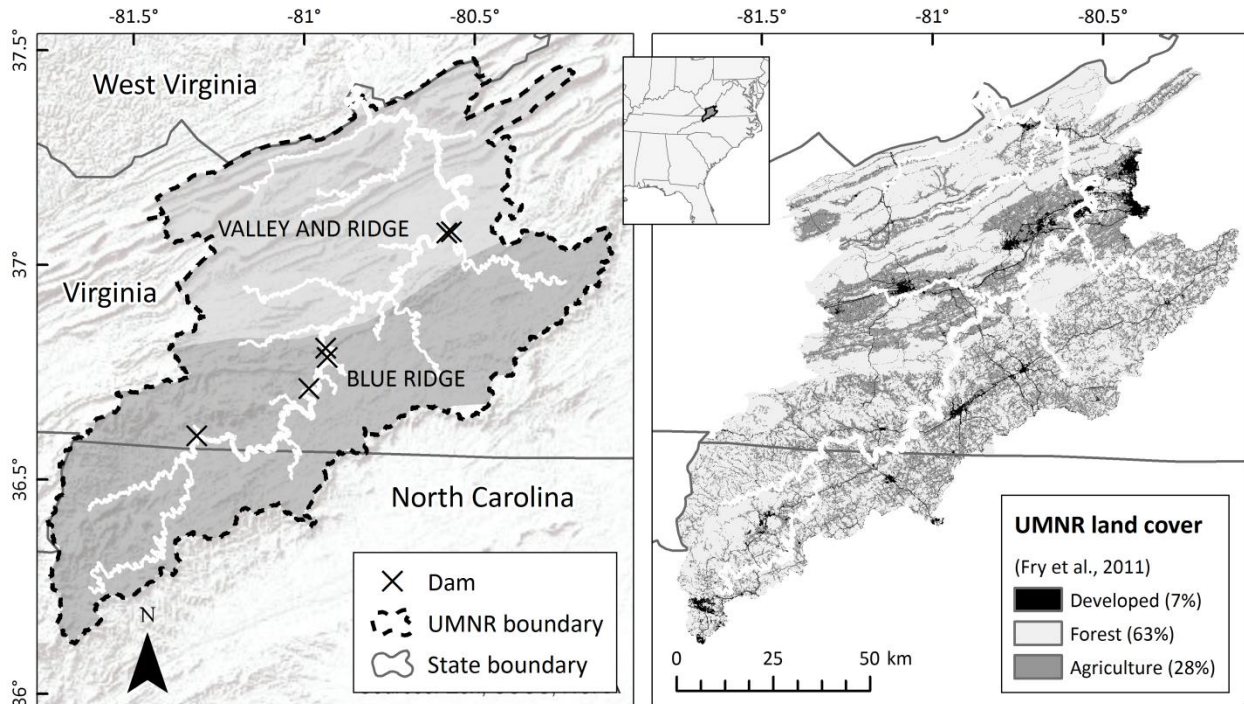
Fig. 3.4 The upper and middle New River (UMNR) study area comprised the Virginia and North Carolina portions of the New River drainage. Left map shows physiographic provinces and major dams. Right map shows 2006 land cover *sensu* Fry *et al.* (2011).
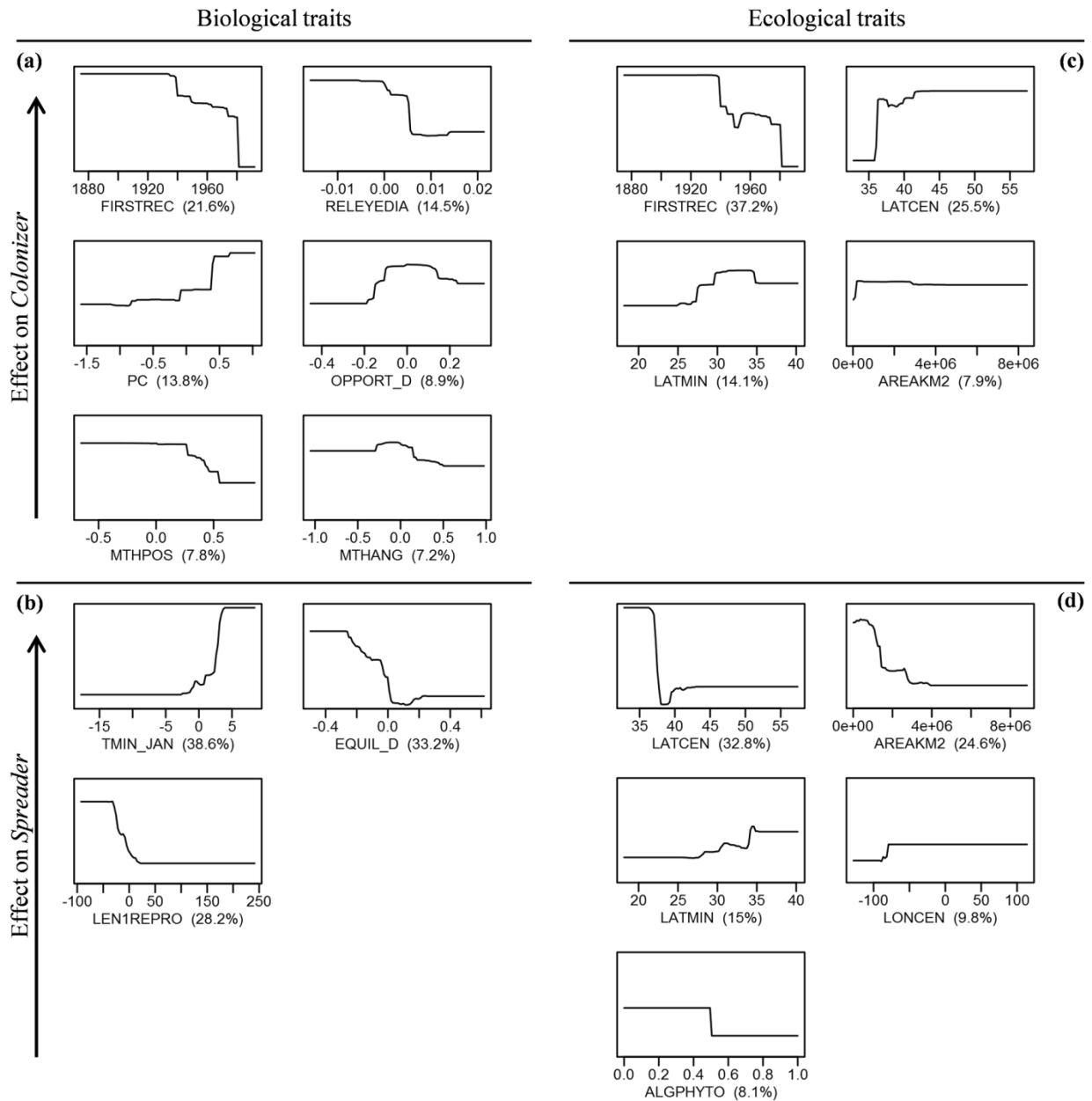
Fig. 3.5 Partial dependence plots from boosted classification tree analyses for the contribution of biological (a, b) and ecological (c, d) species traits (Table S5) to responses of two binary variables *Colonizer* (a, c) and *Spreader* (b, d) for 39 introduced and 35 native fish species. Y-axes show the partial effect of a trait on the response after accounting for the average effects of all other variables in the model. All plots within a panel share a common Y-axis scale. The relative influence (%) of a trait to the modeled response is included in the X-axis label. Only traits having >7% relative influence are shown. X-axis values of biological traits represent residuals from phylogenetic eigenvector regression. *FIRSTREC* was an introduction attribute included in both analyses for *Colonizer*.

86
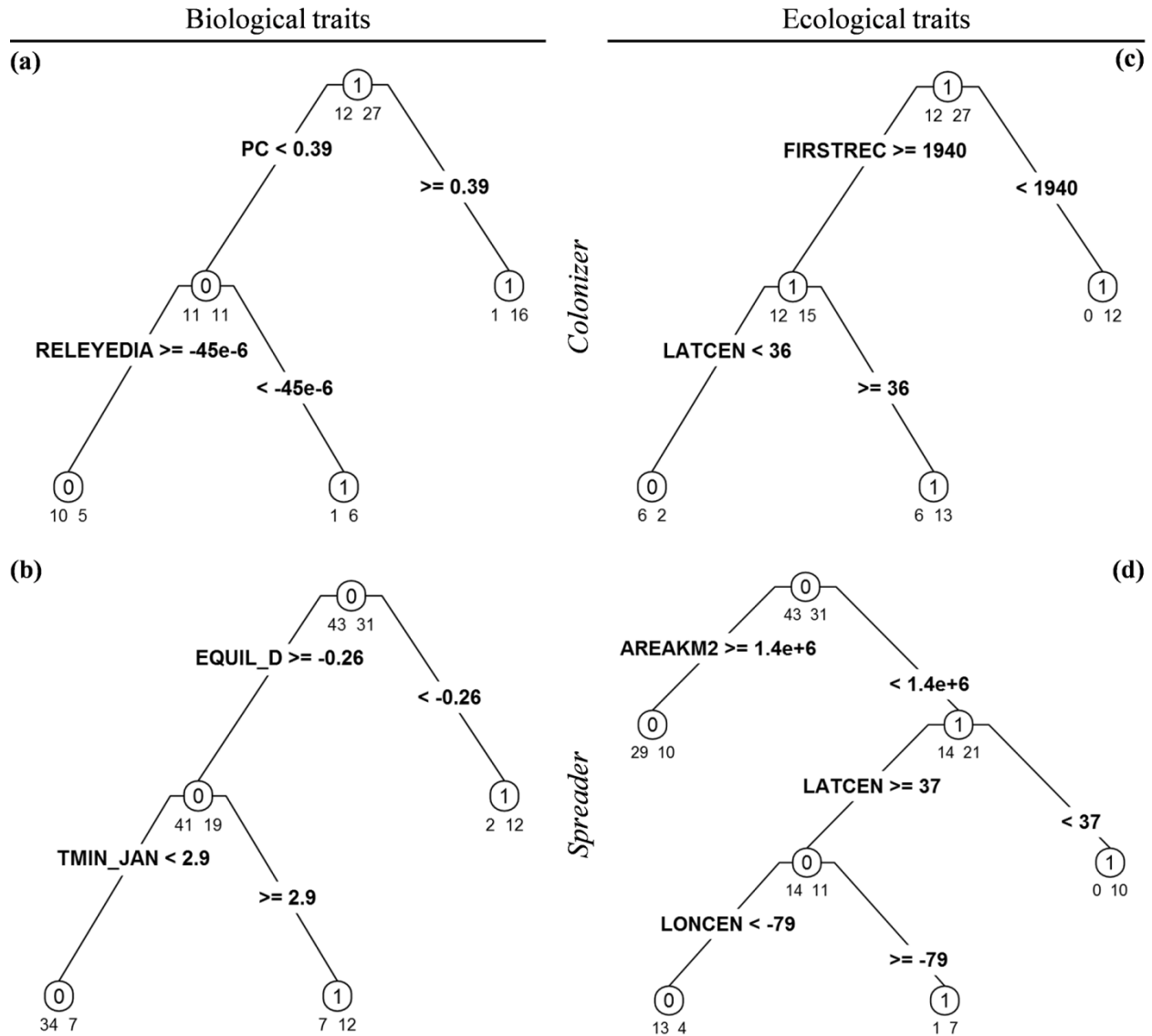
Fig. 3.6 Optimally pruned classification trees for the contribution of biological (a, b) and ecological (c, d) traits (Table S5) of 39 established introduced and 35 native fish species reported from tributaries of the upper and middle New River to responses of two binary variables, *Colonizer* (a, c) and *Spreader* (b, d). Labels inside nodes (circles) indicate the predicted response class (0 = weak colonizer/nonspreader, 1 = strong colonizer/spreader). Labels below nodes indicate the observed number of species in each response class (0, 1). Splits are labeled 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 *Colonizer*.
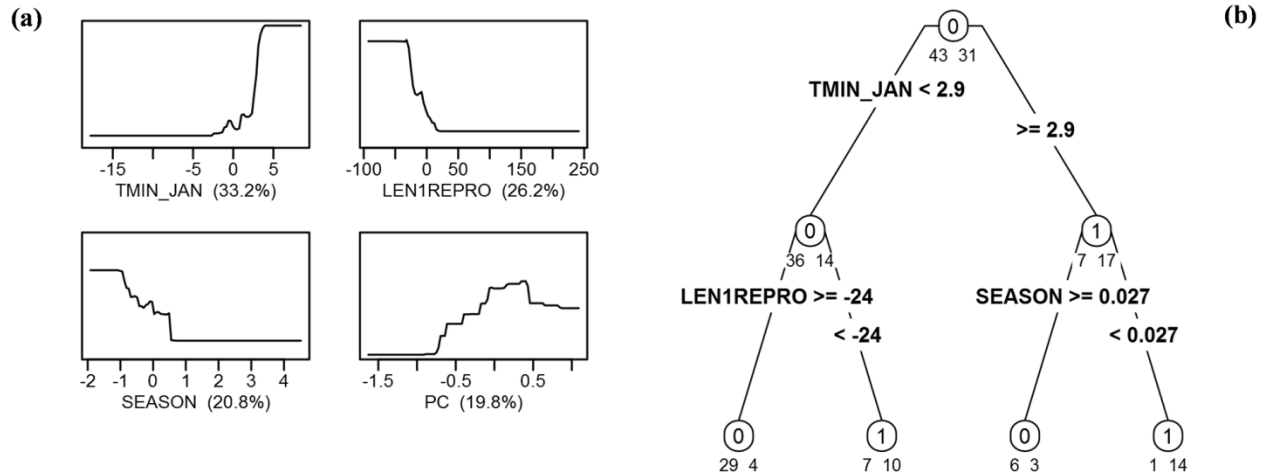
Fig. 3.7 Contribution of biological traits (Table S5), excluding EQUIL_D, OPPORT_D, and PERIOD_D, to the response of the binary variable *Spreader* for 39 introduced and 35 native fish species reported from upper and middle New River tributaries. Partial dependence plots from boosted classification trees analysis (a), and an optimally pruned classification tree (b), are formatted as in Figs. 3.5 and 3.6, respectively. These three Winemiller & Rose (1992) multivariate life history traits were excluded here to allow further interpretation of the effect of individual life history traits on *Spreader*.

CONCLUSIONS

In this study I developed a quantitative framework to detect spatiotemporal trends in species distributions using long-term presence data aggregated by subwatersheds (Chapter 2). Then I examined the contribution of species traits to invasion success during the colonization and spread stages for native and introduced fish species inhabiting UMNR tributaries (Chapter 3). Based on the presumed biological and ecological effects of the traits that have most influenced invasion outcomes, I made inferences about underlying ecological filters and human influences driving stream fish distributional trends. This study provides a baseline for complementary investigations of landscape and fish community characteristics that determine the invasion resistance of individual subwatersheds, as well as causes of declines of native species.

A key finding of Chapter 2 was that most UMNR spreaders are spreading exponentially. Evidence for an upper asymptote to the spread of introduced species was inconclusive even after >50 generations since initial detection. This finding suggests that the full impact of invaders on native and naturalized species and ecosystems is yet to be realized in the UMNR. I found a declining trend in the distribution of four native UMNR fish species. In addition to distributional trends, future studies should examine changes in relative abundance of species over time and compare the effects of alternate stressors on species of concern (e.g., invasive species versus habitat changes, e.g., Light & Marchetti, 2007).

Contrary to the popular perception that abiotic, rather than biotic factors are the principal filtering mechanisms of broad-scale species distribution (Poff, 1997; Peterson *et al.*, 2011) and principal determinants of fish invasion success (Moyle & Light, 1996), I found parental care, especially nest spawning and nest-association, to be an important predictor of invasion success over a large spatial scale (10,000 km^2 drainage basin). Strong spreaders (Chapter 2) and strong colonizers (Chapter 3) were disproportionately represented by nest builders and associates that spawn in nests built by other species, and parental care (which underlies the success of nest spawners and nest-associates) was a prominent predictor of colonization and spread. This finding corroborates other recent studies identifying nest spawning and nest-association as an important broad-scale biotic factor in structuring lotic cyprinid communities (Hitt & Roberts, 2012; Pendleton *et al.*, 2012; Peoples & Frimpong, 2013; Peoples, Blanc & Frimpong, 2015). Nest spawning/association per se appears to be a principal mechanism mediating the rapid spread of several native invaders in the UMNR. I recommend follow-up studies on the role of spawning-

mound builders such as *Nocomis* species in triggering invasional meltdowns (Simberloff & Von Holle, 1999) by facilitating groups of native and introduced nest associates.

Suites of biological traits that predicted colonization and spread may reflect the influence of human land-use practices in the UMNR. Successful colonization and spread were both associated with equilibrium life history traits, which are expected to confer competitive advantages in stable, predictable environments (Winemiller, 2005). Chronic siltation due to riparian deforestation, and perhaps flow regulation by numerous dams, may have given rise to novel environmental conditions favoring equilibrium strategists. Benthic feeding traits, especially smaller eye diameter, expressed by successful colonizers imply that species able to locate food using senses other than sight were favored through the colonization stage. A plausible hypothesis is that land use practices have increased suspended sediment levels and decreased water transparency in UMNR tributaries. Finally, the relatively warmer native ranges of successful spreaders suggested that human activities such as riparian deforestation have warmed UMNR tributaries, thereby altering a key ecological filter. These findings suggest that human land-use practices have facilitated invaders that probably would not have been as successful under natural conditions. Invasion resistance may therefore be boosted by restoration of riparian forest, excluding livestock from streams, stabilizing eroding banks, and other practices that restore natural thermal, hydrologic, and sediment regimes in degraded reaches. Further studies that compare environmental conditions of highly invaded and minimally invaded areas (e.g., subwatersheds), or that model the spatial distribution of strong versus weak colonizers and spreaders using watershed and human-influence attributes, are needed to confirm these speculations.

References

Hitt N.P. & Roberts J.H. (2012) Hierarchical spatial structure of stream fish colonization and extinction. *Oikos*, **121**, 127-137.

Light T. & Marchetti M.P. (2007) Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology*, **21**, 434–446.

Moyle P.B. & Light T. (1996) Fish invasions in California: Do abiotic factors determine success? *Ecology*, **77**, 1666–1670.

Pendleton R.M., Pritt J.J., Peoples B.K. & Frimpong E.A. (2012) The strength of *Nocomis* nest association contributes to patterns of rarity and commonness among New River, Virginia cyprinids. *American Midland Naturalist*, **168**, 202-212.

Peoples B.K., Blanc L.A. & Frimpong E.A. (2015) Lotic cyprinid communities can be structured as nest webs and predicted by the stress-gradient hypothesis. *Journal of Animal Ecology*, **84**, 1666–1677.

Peoples B.K. & Frimpong E.A. (2013) Evidence of mutual benefits of nest association among freshwater cyprinids and implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **23**, 911–923.

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M. *et al.* (2011) Niches and geographic distributions. Chapter 3 In: *Ecological Niches and Geographic Distributions.* Monographs in Population Biology, **49**. Princeton University Press, Princeton, New Jersey.

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

Simberloff D. & Von Holle B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Winemiller K.O. (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 872–885.

Table S1 Fish introductions to the New River drainage. I = introduced; IP = regarded as introduced, but possibly native; IF = failed introduction.

Species	Status	1st record	Source[a]	Species	Status	1st record	Source[a]
Amia calva (bowfin)	I	1953	12	*A. melas* (black bullhead)	IP	1939	7
Dorosoma cepedianum (gizzard shad)*	I	1985	1	*Salvelinus namaycush* (lake trout)	IF	1889	7
D. petenense (threadfin shad)	IF	1949	12	*Salmo trutta* (brown trout)	I	1962	12
Alosa pseudoharengus (alewife)	I	1968	7	*Oncorhynchus clarkii* (cutthroat trout)	IF	~1894	7
A. sapidissima (American shad)	IF	1873	7	*O. mykiss* (rainbow trout)	I	1880	7
Esox masquinongy (muskellunge)	I	1963	7	*O. tshawytscha* (Chinook salmon)	IF	~1880	7
E. niger (chain pickerel)*	I	1953	12	*Labidesthes sicculus* (brook silverside)	I	~1970	7
Cyprinus carpio (common carp)	I	1885	7	*Gambusia holbrooki* (Eastern mosquitofish)*	I	2008	3
Carassius auratus (goldfish)*	I	1990	12	*Morone americana* (white perch)*	I	2006	2
Ctenopharyngodon idella (grass carp)*	I	1991	9	*M. saxatilis* (striped bass)	I	1969	8
Tinca tinca (tench)	IF	~1886	7	*M.chrysops* (white bass)	I	1957	12
Notemigonus crysoleucas (golden shiner)	I	1949	7	*Ambloplites rupestris* (rock bass)	I	1875	7
Scardinius erythrophthalmus (rudd)*	IF	1991	5	*A. cavifrons* (Roanoke bass)	IF	1879	7
Chrosomus erythrogaster (Southern redbelly dace)*	I	2003	13	*Pomoxis nigromaculatus* (black crappie)	I	1949	12
Exoglossum maxillingua (cutlips minnow)	IP	1956	7	*P. annularis* (white crappie)	I	1952	12
Hybopsis hypsinotus (highback chub)*	I	1999	11	*Micropterus dolomieu* (smallmouth bass)	I	1878	7
Cyprinella galactura (whitetail shiner)	IP	1954	7	*M. punctulatus* (spotted bass)	I	1928	7
Luxilus coccogenis (warpaint shiner)	IP	1941	10	*M. salmoides* (largemouth bass)	I	1928	7
L. cerasinus (crescent shiner)	IP	1951	7	*Lepomis gulosus* (warmouth)	IF	1975	12
Notropis leuciodus (Tennessee shiner)	IP	1963	10	*L. auritus* (redbreast sunfish)	I	1939	7
N. rubricroceus (saffron shiner)	IP	1963	7	*L. megalotis* (longear sunfish)	I	1928	7
N. chiliticus (redlip shiner)	IP	1963	10	*L. macrochirus* (bluegill)	I	1936	7
N. atherinoides (emerald shiner)*	I	1962	4	*L. gibbosus* (pumpkinseed)	I	1920	7
N. telescopus (telescope shiner)	IP	1958	7	*L. microlophus* (redear sunfish)*	I	1992	12
N. hudsonius (spottail shiner)	IP	1948	7	*Perca flavescens* (yellow perch)	I	1917	7
N. procne (swallowtail shiner)	IP	1971	7	*Percina maculata* (blackside darter)*	IP	2003	13
Pimephales promelas (fathead minnow)	I	1958	12	*P. roanoka* (Roanoke darter)	IP	1963	7
Moxostoma cervinum (blacktip jumprock)	IP	1987	7	*Etheostoma variatum* (variegate darter)*	I	2003	13
M. erythrurum (golden redhorse)	IP	1976	7	*E. simoterum* (snubnose darter)*	IP	1976	7
M. anisurum (silver redhorse)*	I	1941	10	*E. olmstedi* (tessellated darter)	I	1986	7
Ameiurus natalis (yellow bullhead)	IP	1976	6	*E. rufilineatum* (redline darter)*	I	2011	12
A. nebulosus (brown bullhead)	IP	1976	6	*E. caeruleum* (rainbow darter)*	IP	1972	7

[a] 1 = Cochran (1992); 2 = J. Copeland, VDGIF, Blacksburg, personal communication; 3 = this study; 4 = Easton and Orth (1994); 5 = Easton, Orth & Burkhead (1993); 6 = Hocutt, Denoncourt & Stauffer (1979); 7 = Jenkins & Burkhead (1994); 8 = J. Kilpatrick, unpubl. data; 9 = Menhinick (1991); 10 = NCSM (2014); 11 = SFCAP (2014); 12 = VAFWIS (2013); 13 = D. Wellman, unpubl. data.

Status follows Jenkins & Burkhead (1994), except that *E. simoterum* and *E. caeruleum* were regarded as probably native, but their late discovery and subsequent spread suggest they were likely introduced (M. Pinder, VDGIF, Blacksburg, personal communication). An asterisk (*) indicates an addition to introductions listed by Jenkins & Burkhead (1994).

Table S2 Catch per unit effort (CPUE) time-series data for upper and middle New River stream fishes. Time periods: 1 = 1938–1953 (N_1 = 56 HUC12s sampled); period 2 = 1954–1962 (N_2 = 58); period 3 = 1963–1969 (N_3 = 54); period 4 = 1970–1976 (N_4 = 56); period 5 = 1977–1983 (N_5 = 65); period 6 = 1984–1996 (N_6 = 64); period 7 = 1997–1998 (N_7 = 70); period 8 = 1999–2007 (N_8 = 68); period 9 = 2008–2011 (N_9 = 71); period 10 = 2012–2014 (N_{10} = 64). CPUE = n_i / N_i, where n_i = the number of HUC12s the given species was detected in during time period i. Periods having multiple leading zeros in CPUE, as indicated by CPUE = "-", were excluded from the regressions of CPUE by time period. Species codes are defined in Table 2.1.

Species	Period	n_i	CPUE	Species	Period	n_i	CPUE	Species	Period	n_i	CPUE
AmCalv	1	0	0	AmRupe	1	18	0.321	ChOrea	1	12	0.214
	2	1	0.017		2	34	0.586		2	15	0.259
	3	0	0		3	24	0.444		3	10	0.185
	4	0	0		4	19	0.339		4	28	0.5
	5	0	0		5	19	0.292		5	26	0.4
	6	0	0		6	37	0.578		6	35	0.547
	7	1	0.014		7	39	0.557		7	21	0.3
	8	0	0		8	48	0.706		8	33	0.485
	9	0	0		9	51	0.718		9	44	0.62
	10	0	0		10	48	0.75		10	48	0.75
AmMela	1	0	-	CaAnom	1	37	0.661	ClFund	1	15	0.268
	2	0	0		2	45	0.776		2	24	0.414
	3	1	0.019		3	39	0.722		3	18	0.333
	4	0	0		4	32	0.571		4	29	0.518
	5	0	0		5	37	0.569		5	33	0.508
	6	0	0		6	50	0.781		6	34	0.531
	7	0	0		7	45	0.643		7	20	0.286
	8	0	0		8	54	0.794		8	34	0.5
	9	2	0.028		9	59	0.831		9	43	0.606
	10	1	0.016		10	60	0.938		10	49	0.766
AmNata	1	0	-	CaAura	1	0	-	CoBair	1	19	0.339
	2	0	-		2	0	-		2	27	0.466
	3	0	-		3	0	-		3	20	0.37
	4	0	-		4	0	-		4	29	0.518
	5	0	-		5	0	0		5	25	0.385
	6	0	0		6	2	0.031		6	32	0.5
	7	1	0.014		7	0	0		7	25	0.357
	8	0	0		8	0	0		8	39	0.574
	9	2	0.028		9	0	0		9	36	0.507
	10	4	0.063		10	0	0		10	40	0.625
AmNebu	1	0	-	CaComm	1	30	0.536	CoKana	1	8	0.143
	2	0	-		2	36	0.621		2	7	0.121
	3	0	0		3	33	0.611		3	1	0.019
	4	1	0.018		4	27	0.482		4	10	0.179
	5	0	0		5	30	0.462		5	1	0.015
	6	0	0		6	35	0.547		6	13	0.203
	7	2	0.029		7	20	0.286		7	3	0.043
	8	0	0		8	36	0.529		8	20	0.294
	9	7	0.099		9	40	0.563		9	8	0.113
	10	3	0.047		10	40	0.625		10	12	0.188

-continued-

93

Table S2.–Page 2 of 6.

Species	Period	n_i	CPUE	Species	Period	n_i	CPUE	Species	Period	n_i	CPUE
CyCarp	1	0	-	EtCaer	1	0	-	EtOsbu	1	4	0.071
	2	0	0		2	0	-		2	4	0.069
	3	8	0.148		3	0	-		3	2	0.037
	4	0	0		4	0	-		4	1	0.018
	5	0	0		5	0	-		5	1	0.015
	6	1	0.016		6	0	0		6	2	0.031
	7	2	0.029		7	1	0.014		7	2	0.029
	8	5	0.074		8	1	0.015		8	2	0.029
	9	3	0.042		9	3	0.042		9	4	0.056
	10	1	0.016		10	7	0.109		10	6	0.094
CyGala	1	0	0	EtFlab	1	43	0.768	EtSimo	1	0	-
	2	8	0.138		2	40	0.69		2	0	-
	3	3	0.056		3	34	0.63		3	0	-
	4	6	0.107		4	41	0.732		4	0	-
	5	1	0.015		5	40	0.615		5	0	0
	6	10	0.156		6	48	0.75		6	5	0.078
	7	14	0.2		7	56	0.8		7	5	0.071
	8	14	0.206		8	53	0.779		8	4	0.059
	9	14	0.197		9	60	0.845		9	5	0.07
	10	13	0.203		10	58	0.906		10	7	0.109
CySpil	1	5	0.089	EtKana	1	17	0.304	ExLaur	1	18	0.321
	2	8	0.138		2	18	0.31		2	28	0.483
	3	2	0.037		3	14	0.259		3	17	0.315
	4	5	0.089		4	14	0.25		4	7	0.125
	5	4	0.062		5	6	0.092		5	11	0.169
	6	3	0.047		6	17	0.266		6	11	0.172
	7	3	0.043		7	18	0.257		7	8	0.114
	8	4	0.059		8	17	0.25		8	10	0.147
	9	6	0.085		9	33	0.465		9	18	0.254
	10	6	0.094		10	33	0.516		10	15	0.234
EsNige	1	1	0.018	EtNigr	1	0	-	ExMaxi	1	0	-
	2	0	0		2	0	-		2	0	0
	3	0	0		3	0	-		3	1	0.019
	4	0	0		4	0	-		4	2	0.036
	5	0	0		5	0	0		5	0	0
	6	0	0		6	4	0.063		6	5	0.078
	7	1	0.014		7	3	0.043		7	1	0.014
	8	0	0		8	4	0.059		8	4	0.059
	9	1	0.014		9	6	0.085		9	5	0.07
	10	0	0		10	5	0.078		10	7	0.109
EtBlen	1	17	0.304	EtOlms	1	0	-	HyNigr	1	38	0.679
	2	19	0.328		2	0	-		2	45	0.776
	3	7	0.13		3	0	0		3	40	0.741
	4	12	0.214		4	1	0.018		4	32	0.571
	5	6	0.092		5	0	0		5	24	0.369
	6	14	0.219		6	1	0.016		6	41	0.641
	7	29	0.414		7	3	0.043		7	46	0.657
	8	20	0.294		8	4	0.059		8	49	0.721
	9	23	0.324		9	4	0.056		9	50	0.704
	10	24	0.375		10	4	0.063		10	52	0.813

-continued-

Table S2.–Page 3 of 6.

Species	Period	n_i	CPUE	Species	Period	n_i	CPUE	Species	Period	n_i	CPUE
IcPunc	1	0	-	LeMega	1	0	0	LuCocc	1	2	0.036
	2	0	-		2	1	0.017		2	1	0.017
	3	0	0		3	1	0.019		3	1	0.019
	4	2	0.036		4	0	0		4	1	0.018
	5	0	0		5	0	0		5	3	0.046
	6	2	0.031		6	0	0		6	4	0.063
	7	0	0		7	0	0		7	0	0
	8	0	0		8	1	0.015		8	1	0.015
	9	0	0		9	0	0		9	8	0.113
	10	0	0		10	0	0		10	10	0.156
LeAuri	1	7	0.125	LeMicr	1	0	-	LyArde	1	12	0.214
	2	9	0.155		2	0	-		2	14	0.241
	3	8	0.148		3	0	-		3	7	0.13
	4	4	0.071		4	0	-		4	15	0.268
	5	1	0.015		5	0	0		5	6	0.092
	6	14	0.219		6	1	0.016		6	17	0.266
	7	19	0.271		7	0	0		7	5	0.071
	8	29	0.426		8	1	0.015		8	16	0.235
	9	32	0.451		9	1	0.014		9	12	0.169
	10	27	0.422		10	0	0		10	20	0.313
LeCyan	1	2	0.036	LuAlbe	1	15	0.268	MiDolo	1	18	0.321
	2	6	0.103		2	28	0.483		2	29	0.5
	3	3	0.056		3	7	0.13		3	25	0.463
	4	2	0.036		4	18	0.321		4	10	0.179
	5	1	0.015		5	10	0.154		5	14	0.215
	6	13	0.203		6	28	0.438		6	34	0.531
	7	3	0.043		7	10	0.143		7	33	0.471
	8	12	0.176		8	26	0.382		8	34	0.5
	9	13	0.183		9	27	0.38		9	39	0.549
	10	18	0.281		10	30	0.469		10	28	0.438
LeGibb	1	1	0.018	LuCera	1	6	0.107	MiPunc	1	0	-
	2	3	0.052		2	14	0.241		2	0	0
	3	4	0.074		3	3	0.056		3	2	0.037
	4	1	0.018		4	10	0.179		4	1	0.018
	5	2	0.031		5	6	0.092		5	0	0
	6	9	0.141		6	17	0.266		6	1	0.016
	7	3	0.043		7	23	0.329		7	1	0.014
	8	4	0.059		8	15	0.221		8	1	0.015
	9	6	0.085		9	11	0.155		9	4	0.056
	10	4	0.063		10	23	0.359		10	5	0.078
LeMacr	1	7	0.125	LuChry	1	0	0	MiSalm	1	5	0.089
	2	8	0.138		2	2	0.034		2	4	0.069
	3	13	0.241		3	2	0.037		3	2	0.037
	4	6	0.107		4	1	0.018		4	3	0.054
	5	3	0.046		5	0	0		5	1	0.015
	6	18	0.281		6	9	0.141		6	7	0.109
	7	9	0.129		7	1	0.014		7	5	0.071
	8	14	0.206		8	5	0.074		8	8	0.118
	9	14	0.197		9	0	0		9	10	0.141
	10	18	0.281		10	0	0		10	11	0.172

-continued-

Species	Period	n_i	CPUE	Species	Period	n_i	CPUE	Species	Period	n_i	CPUE
MoCerv	1	0	-	NoLept	1	20	0.357	NoRube	1	29	0.518
	2	0	-		2	30	0.517		2	18	0.31
	3	0	-		3	19	0.352		3	13	0.241
	4	0	-		4	29	0.518		4	15	0.268
	5	0	0		5	22	0.338		5	12	0.185
	6	2	0.031		6	38	0.594		6	19	0.297
	7	0	0		7	23	0.329		7	3	0.043
	8	1	0.015		8	38	0.559		8	11	0.162
	9	3	0.042		9	54	0.761		9	27	0.38
	10	2	0.031		10	56	0.875		10	16	0.25
NoChil	1	0	-	NoLeuc	1	0	-	NoRubr	1	0	-
	2	0	0		2	0	0		2	0	0
	3	2	0.037		3	1	0.019		3	1	0.019
	4	4	0.071		4	0	0		4	9	0.161
	5	3	0.046		5	0	0		5	10	0.154
	6	4	0.063		6	0	0		6	11	0.172
	7	7	0.1		7	1	0.014		7	7	0.1
	8	6	0.088		8	0	0		8	10	0.147
	9	7	0.099		9	4	0.056		9	20	0.282
	10	8	0.125		10	3	0.047		10	23	0.359
NoCrys	1	2	0.036	NoPhot	1	26	0.464	NoScab	1	22	0.393
	2	1	0.017		2	28	0.483		2	19	0.328
	3	0	0		3	18	0.333		3	14	0.259
	4	0	0		4	12	0.214		4	14	0.25
	5	1	0.015		5	8	0.123		5	12	0.185
	6	2	0.031		6	13	0.203		6	13	0.203
	7	0	0		7	9	0.129		7	7	0.1
	8	0	0		8	12	0.176		8	9	0.132
	9	0	0		9	19	0.268		9	24	0.338
	10	1	0.016		10	12	0.188		10	20	0.313
NoHuds	1	0	-	NoPlat	1	16	0.286	NoTele	1	0	0
	2	0	-		2	23	0.397		2	5	0.086
	3	0	0		3	16	0.296		3	6	0.111
	4	2	0.036		4	14	0.25		4	8	0.143
	5	0	0		5	9	0.138		5	3	0.046
	6	2	0.031		6	17	0.266		6	12	0.188
	7	2	0.029		7	7	0.1		7	8	0.114
	8	4	0.059		8	17	0.25		8	18	0.265
	9	10	0.141		9	23	0.324		9	16	0.225
	10	1	0.016		10	28	0.438		10	13	0.203
NoInsi	1	7	0.125	NoProc	1	0	-	NoVolu	1	9	0.161
	2	13	0.224		2	0	-		2	7	0.121
	3	14	0.259		3	0	0		3	0	0
	4	7	0.125		4	4	0.071		4	6	0.107
	5	6	0.092		5	0	0		5	5	0.077
	6	22	0.344		6	0	0		6	6	0.094
	7	27	0.386		7	0	0		7	3	0.043
	8	21	0.309		8	2	0.029		8	9	0.132
	9	17	0.239		9	1	0.014		9	5	0.07
	10	30	0.469		10	1	0.016		10	11	0.172

-continued-

Species	Period	n_i	CPUE	Species	Period	n_i	CPUE	Species	Period	n_i	CPUE
OnMyki	1	4	0.071	PeRoan	1	0	-	PoNigr	1	0	-
	2	6	0.103		2	0	-		2	0	-
	3	6	0.111		3	0	0		3	0	0
	4	14	0.25		4	2	0.036		4	1	0.018
	5	17	0.262		5	2	0.031		5	0	0
	6	9	0.141		6	2	0.031		6	0	0
	7	14	0.2		7	3	0.043		7	0	0
	8	19	0.279		8	7	0.103		8	0	0
	9	25	0.352		9	8	0.113		9	2	0.028
	10	31	0.484		10	4	0.063		10	0	0
PeCapr	1	0	-	PhTere	1	22	0.393	RhAtra	1	37	0.661
	2	0	-		2	18	0.31		2	39	0.672
	3	0	-		3	18	0.333		3	33	0.611
	4	0	-		4	13	0.232		4	36	0.643
	5	0	-		5	11	0.169		5	45	0.692
	6	0	0		6	15	0.234		6	38	0.594
	7	3	0.043		7	18	0.257		7	28	0.4
	8	0	0		8	9	0.132		8	46	0.676
	9	1	0.014		9	22	0.31		9	46	0.648
	10	1	0.016		10	20	0.313		10	50	0.781
PeFlav	1	1	0.018	PiNota	1	25	0.446	RhCata	1	23	0.411
	2	0	0		2	21	0.362		2	31	0.534
	3	1	0.019		3	8	0.148		3	29	0.537
	4	0	0		4	12	0.214		4	20	0.357
	5	0	0		5	10	0.154		5	16	0.246
	6	0	0		6	16	0.25		6	26	0.406
	7	1	0.014		7	7	0.1		7	26	0.371
	8	1	0.015		8	23	0.338		8	24	0.353
	9	0	0		9	17	0.239		9	41	0.577
	10	0	0		10	19	0.297		10	38	0.594
PeGymn	1	12	0.214	PiProm	1	0	-	SaFont	1	5	0.089
	2	7	0.121		2	0	-		2	5	0.086
	3	7	0.13		3	0	-		3	7	0.13
	4	10	0.179		4	0	-		4	17	0.304
	5	10	0.154		5	0	0		5	24	0.369
	6	14	0.219		6	1	0.016		6	14	0.219
	7	16	0.229		7	2	0.029		7	8	0.114
	8	11	0.162		8	2	0.029		8	8	0.118
	9	22	0.31		9	4	0.056		9	14	0.197
	10	20	0.313		10	1	0.016		10	14	0.219
PeOxyr	1	3	0.054	PoAnnu	1	0	0	SaTrut	1	0	0
	2	6	0.103		2	1	0.017		2	1	0.017
	3	2	0.037		3	0	0		3	1	0.019
	4	6	0.107		4	1	0.018		4	7	0.125
	5	3	0.046		5	0	0		5	12	0.185
	6	3	0.047		6	0	0		6	10	0.156
	7	3	0.043		7	0	0		7	11	0.157
	8	3	0.044		8	0	0		8	17	0.25
	9	3	0.042		9	0	0		9	24	0.338
	10	0	0		10	0	0		10	27	0.422

-continued-

Table S2.–Page 6 of 6.

Species	Period	n_i	CPUE	Species	Period	n_i	CPUE
SeAtro	1	26	0.464	ThRhot	1	1	0.018
	2	27	0.466		2	0	0
	3	20	0.37		3	0	0
	4	16	0.286		4	0	0
	5	14	0.215		5	1	0.015
	6	21	0.328		6	2	0.031
	7	12	0.171		7	1	0.014
	8	20	0.294		8	1	0.015
	9	31	0.437		9	1	0.014
	10	28	0.438		10	5	0.078

Table S3 Values used to classify spreader status and identify the best model of spread/decline for 74 fishes of upper and middle New River tributaries. The following 6 models were fitted to the catch per unit effort (CPUE) time-series data (Table S2) and compared using Akaike's Information Criterion corrected for small samples (AICc) (see *Methods*): intercept-only (null); linear (lin), 2-parameter exponential (exp2); 3-parameter exponential (exp3); 3-parameter logistic (log3); and 4-parameter logistic (log4). Symbols & abbreviations: n = number of time periods with CPUE data; Δ_i = AICc$_i$ − AICc$_{min}$; w_i = Akaike weight (probability that model i is the best model); β_1 = estimated slope/growth-rate term of fitted model; β_1 LCL/UCL = 90% lower/upper confidence limit on β_1; "-" indicates the fitting algorithm did not converge for the given term; Species codes are defined in Table 2.1.

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
AmCalv	10	null	-67.12	0	0.7712	NA	NA	NA
		lin	-63.29	3.836	0.1133	-0.000065	-0.000265	0.000135
		exp2	-63.23	3.897	0.1099	-0.017313	-	-
		exp3	-57.29	9.836	0.0056	-0.000039	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
AmMela	9	null	-50.87	0	0.5956	NA	NA	NA
		exp2	-49.53	1.344	0.3042	0.135953	-0.003995	0.594144
		lin	-47.08	3.797	0.0892	0.000187	-0.000203	0.000576
		exp3	-42.89	7.980	0.0110	0.168746	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
AmNata	5	null	-13.43	0	0.9864	NA	NA	NA
		exp2	-4.81	8.618	0.0133	0.260962	0.114559	-
		lin	2.58	16.004	0.0003	0.002434	-0.000556	0.005424
		log4	-	-	-	-	-	-
		exp3	-	-	-	0.201840	-	-
		log3	-	-	-	3.344965	-	-
AmNebu	8	null	-25.72	0	0.4859	NA	NA	NA
		exp2	-25.12	0.606	0.3588	0.092588	0.010932	0.368767
		lin	-23.42	2.300	0.1538	0.001211	-0.000133	0.002555
		exp3	-14.08	11.638	0.0014	-0.000155	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
AmRupe	10	exp2	-7.62	0	0.5606	0.012855	0.006065	0.020535
		lin	-6.34	1.278	0.2959	0.006022	0.002571	0.009472
		exp3	-3.92	3.697	0.0883	0.056950	-0.005509	0.173792
		null	-2.22	5.394	0.0378	NA	NA	NA
		log3	-0.24	7.380	0.0140	0.024789	-	0.070575
		log4	2.59	10.209	0.0034	3.247758	-	26.175033
CaAnom	10	null	-9.69	0	0.3817	NA	NA	NA
		exp2	-9.33	0.352	0.3201	0.004514	0.000236	0.008973
		lin	-9.00	0.687	0.2708	0.003024	0.000003	0.006045
		exp3	-3.00	6.690	0.0135	-0.000044	-	-
		log3	-2.55	7.137	0.0108	0.013596	-	-
		log4	-0.12	9.568	0.0032	4.584056	-	25.553462
CaAura	6	null	-28.41	0	0.9849	NA	NA	NA
		lin	-18.74	9.661	0.0079	-0.000260	-0.001409	0.000890
		exp2	-18.57	9.832	0.0072	-0.023149	-	-

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
CaAura		log3	8.53	36.935	0.0000	-18.017095	-	-
(cont.)		exp3	11.26	39.662	0.0000	-0.000071	-	-
		log4	-	-	-	-	-	-
CaComm	10	null	-12.82	0	0.7906	NA	NA	NA
		exp2	-8.68	4.135	0.1000	-0.001130	-0.007137	0.005005
		lin	-8.67	4.145	0.0995	-0.000556	-0.003626	0.002514
		exp3	-2.67	10.145	0.0050	0.000010	-	-
		log3	-2.67	10.146	0.0050	-0.002216	-	-
		log4	-	-	-	-	-	-
ChOrea	10	exp2	-7.68	0	0.5431	0.018025	0.009501	0.028372
		lin	-7.03	0.655	0.3913	0.007060	0.003727	0.010394
		exp3	-1.90	5.783	0.0301	0.038316	-0.047515	0.387207
		log3	-1.07	6.610	0.0199	0.030577	0.013909	0.131933
		null	-0.53	7.149	0.0152	NA	NA	NA
		log4	7.74	15.421	0.0002	20.360498	-	76.946853
ClFund	10	exp2	-6.99	0	0.4112	0.011074	0.003575	0.019616
		lin	-6.70	0.288	0.3562	0.004923	0.001535	0.008311
		null	-4.50	2.487	0.1186	NA	NA	NA
		exp3	-4.08	2.915	0.0957	0.206801	-0.028893	-
		log3	-0.64	6.352	0.0172	0.019999	-	-
		log4	4.89	11.880	0.0011	2.983827	-	92.790479
CoBair	10	exp2	-14.98	0	0.3973	0.006727	0.001713	0.012057
		lin	-14.73	0.245	0.3515	0.002972	0.000705	0.005240
		null	-13.47	1.514	0.1864	NA	NA	NA
		exp3	-10.70	4.278	0.0468	0.100144	-0.073157	-
		log3	-8.75	6.232	0.0176	0.012081	-	-
		log4	-1.68	13.295	0.0005	7.776246	-	255.565590
CoKana	10	null	-15.29	0	0.6734	NA	NA	NA
		exp2	-12.46	2.833	0.1633	0.013007	-0.008579	0.046577
		lin	-12.23	3.064	0.1455	0.001409	-0.001161	0.003979
		exp3	-6.83	8.466	0.0098	0.056736	-	-
		log3	-6.43	8.862	0.0080	0.014745	-	-
		log4	-	-	-	-	-	-
CyCarp	9	null	-24.00	0	0.8400	NA	NA	NA
		exp2	-19.25	4.754	0.0780	-0.005296	-0.159444	0.319855
		lin	-19.24	4.760	0.0778	-0.000171	-0.001999	0.001656
		log3	-12.05	11.955	0.0021	-0.005476	-	-
		exp3	-12.04	11.960	0.0021	0.000039	-	-
		log4	-	-	-	-	-	-
CyGala	10	exp2	-23.65	0	0.4702	0.024889	0.012004	0.042636
		lin	-23.58	0.068	0.4544	0.002984	0.001527	0.004441
		log3	-17.88	5.763	0.0264	0.041120	0.017918	0.594940
		exp3	-17.80	5.846	0.0253	0.013594	-0.066263	0.104761
		null	-17.52	6.123	0.0220	NA	NA	NA
		log4	-12.41	11.236	0.0017	0.573792	-	-
CySpil	10	null	-36.60	0	0.7209	NA	NA	NA

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
CySpil		exp2	-33.29	3.307	0.1380	-0.006298	-0.020019	0.006979
(cont.)		lin	-33.14	3.457	0.1280	-0.000404	-0.001307	0.000500
		log3	-27.28	9.320	0.0068	-0.006733	-	-
		exp3	-27.14	9.458	0.0064	0.000022	-	-
		log4	-	-	-	-	-	-
EsNige	10	null	-64.79	0	0.7943	NA	NA	NA
		exp2	-60.65	4.141	0.1002	-0.016929	-	-
		lin	-60.56	4.231	0.0958	-0.000026	-0.000255	0.000203
		log3	-54.65	10.143	0.0050	-0.016648	-	-
		exp3	-54.56	10.231	0.0048	0.000007	-	-
		log4	-	-	-	-	-	-
EtBlen	10	null	-12.29	0	0.6573	NA	NA	NA
		exp2	-9.57	2.713	0.1692	0.007599	-0.004444	0.021755
		lin	-9.30	2.982	0.1480	0.001689	-0.001286	0.004664
		exp3	-5.03	7.257	0.0175	0.081866	-	-
		log3	-3.47	8.813	0.0080	0.009791	-	-
		log4	-	-	-	-	-	-
EtCaer	5	null	-8.23	0	0.6988	NA	NA	NA
		exp2	-6.54	1.686	0.3007	0.278308	0.186389	-
		lin	6.27	14.495	0.0005	0.004510	0.000185	0.008836
		log4	-	-	-	-	-	-
		exp3	-	-	-	0.200458	-	-
		log3	-	-	-	0.318789	-	0.857214
EtFlab	10	exp2	-16.75	0	0.3320	0.003911	0.001075	0.006818
		lin	-16.32	0.433	0.2674	0.002758	0.000663	0.004853
		exp3	-16.18	0.571	0.2495	0.087059	0.015078	0.378251
		null	-15.01	1.739	0.1391	NA	NA	NA
		log3	-9.61	7.144	0.0093	0.013244	-	0.082442
		log4	-7.13	9.623	0.0027	8.053337	-	34.363303
EtKana	10	exp3	-10.84	0	0.5015	0.204991	0.069808	0.652127
		null	-9.61	1.229	0.2713	NA	NA	NA
		exp2	-7.95	2.886	0.1184	0.010487	-0.002016	0.026393
		lin	-7.31	3.527	0.0860	0.002344	-0.000942	0.005631
		log4	-4.15	6.689	0.0177	0.614871	-	8.932878
		log3	-1.64	9.194	0.0051	0.013255	-	-
EtNigr	6	lin	-19.04	0	0.5528	0.002433	0.001311	0.003554
		null	-17.95	1.084	0.3215	NA	NA	NA
		exp2	-16.07	2.963	0.1257	0.043306	0.014758	0.085202
		log3	10.70	29.732	0.0000	0.212301	-	-
		exp3	11.00	30.038	0.0000	0.000569	-	-
		log4	-	-	-	4.710289	-	163.016821
EtOlms	8	exp2	-39.35	0	0.5438	0.052281	0.031017	0.083788
		lin	-38.23	1.120	0.3106	0.001433	0.000900	0.001965
		log3	-36.54	2.818	0.1329	0.994383	-	-
		exp3	-30.72	8.635	0.0073	0.033015	-0.027622	0.110035
		null	-30.12	9.234	0.0054	NA	NA	NA
		log4	-20.89	18.465	0.0001	0.862475	-	5.185068

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
EtOsbu	10	null	-39.83	0	0.8061	NA	NA	NA
		exp2	-35.55	4.285	0.0946	0.000305	-0.024545	0.030512
		lin	-35.55	4.285	0.0946	0.000008	-0.000793	0.000809
		exp3	-29.55	10.285	0.0047	-0.000004	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
EtSimo	6	null	-15.96	0	0.7946	NA	NA	NA
		lin	-12.42	3.545	0.1350	0.002540	0.000592	0.004487
		exp2	-11.12	4.847	0.0704	0.037745	0.002973	0.096580
		log3	15.06	31.024	0.0000	0.619667	-	-
		exp3	17.59	33.556	0.0000	0.000304	-	-
		log4	-	-	-	-	-	-
ExLaur	10	exp2	-10.56	0	0.3774	-0.014661	-0.029371	-0.002008
		null	-10.28	0.274	0.3291	NA	NA	NA
		lin	-9.70	0.854	0.2462	-0.002971	-0.005887	-0.000054
		exp3	-5.53	5.021	0.0306	-0.046973	-0.257141	0.044280
		log3	-4.32	6.235	0.0167	-0.018889	-0.162286	-
		log4	-	-	-	-	-	-
ExMaxi	9	exp2	-33.69	0	0.6629	0.049290	0.021257	0.112604
		lin	-31.80	1.890	0.2577	0.001581	0.000671	0.002491
		null	-28.18	5.511	0.0422	NA	NA	NA
		exp3	-26.66	7.032	0.0197	0.069612	-0.042998	0.610951
		log3	-26.42	7.265	0.0175	0.051632	0.020140	0.520020
		log4	-14.61	19.077	0.0000	13.619470	-	59.390589
HyNigr	10	null	-8.49	0	0.7775	NA	NA	NA
		exp2	-4.42	4.074	0.1014	0.001334	-0.004625	0.007515
		lin	-4.40	4.093	0.1004	0.000807	-0.002995	0.004609
		exp3	-0.68	7.809	0.0157	0.174840	-	-
		log3	1.62	10.109	0.0050	0.003330	-	-
		log4	-	-	-	-	-	-
IcPunc	8	null	-38.59	0	0.8476	NA	NA	NA
		lin	-33.91	4.684	0.0815	-0.000307	-0.001005	0.000392
		exp2	-33.61	4.983	0.0702	-0.023386	-	-
		exp3	-24.57	14.018	0.0008	-0.000047	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
LeAuri	10	exp2	-15.80	0	0.7395	0.035485	0.021649	0.055264
		log4	-11.92	3.887	0.1059	2.423298	0.452160	7.302147
		exp3	-11.46	4.341	0.0844	0.058735	0.017835	0.119091
		lin	-10.10	5.701	0.0428	0.005852	0.002993	0.008710
		log3	-9.06	6.742	0.0254	0.049244	0.026776	-
		null	-4.05	11.753	0.0021	NA	NA	NA
LeCyan	10	exp2	-21.09	0	0.7239	0.040466	0.017961	0.086557
		lin	-17.77	3.323	0.1374	0.003055	0.001107	0.005003
		exp3	-16.57	4.520	0.0755	0.085523	0.006394	0.395760
		null	-14.81	6.279	0.0314	NA	NA	NA
		log3	-14.79	6.304	0.0310	0.046105	0.019288	0.285639

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
LeCyan (cont.)		log4	-7.52	13.575	0.0008	10.364697	-	47.053883
LeGibb	10	null	-33.13	0	0.5847	NA	NA	NA
		lin	-31.03	2.096	0.2050	0.000755	-0.000248	0.001759
		exp2	-30.87	2.257	0.1891	0.012439	-0.004747	0.035787
		log3	-25.16	7.966	0.0109	0.052160	-	-
		exp3	-25.03	8.097	0.0102	0.000089	-	-
		log4	-	-	-	-	-	-
LeMacr	10	null	-17.83	0	0.5128	NA	NA	NA
		exp2	-16.35	1.482	0.2445	0.011163	-0.001687	0.027364
		lin	-16.07	1.764	0.2123	0.001728	-0.000393	0.003849
		exp3	-11.19	6.639	0.0186	0.084455	-	-
		log3	-10.29	7.542	0.0118	0.013259	-	-
		log4	-	-	-	-	-	-
LeMega	10	null	-63.09	0	0.7294	NA	NA	NA
		lin	-59.71	3.379	0.1347	-0.000112	-0.000351	0.000127
		exp2	-59.63	3.462	0.1292	-0.018982	-0.120845	0.100528
		exp3	-53.71	9.378	0.0067	0.001961	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
LeMicr	6	null	-33.82	0	0.9838	NA	NA	NA
		lin	-24.30	9.526	0.0084	0.000195	-0.000529	0.000918
		exp2	-24.14	9.677	0.0078	0.018707	-	-
		exp3	5.70	39.527	0.0000	0.000074	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
LuAlbe	10	null	-6.78	0	0.7106	NA	NA	NA
		exp2	-3.51	3.275	0.1382	0.006827	-0.006859	0.023338
		lin	-3.36	3.421	0.1285	0.001831	-0.002173	0.005835
		exp3	0.82	7.599	0.0159	0.153085	-	-
		log3	2.56	9.347	0.0066	0.009273	-	-
		log4	9.80	16.583	0.0002	4.584653	-	-
LuCera	10	null	-12.80	0	0.3658	NA	NA	NA
		exp2	-12.47	0.326	0.3108	0.014064	0.000772	0.031285
		lin	-12.35	0.447	0.2925	0.002658	0.000103	0.005212
		exp3	-6.48	6.319	0.0155	0.018238	-	-
		log3	-6.47	6.332	0.0154	0.017624	-	-
		log4	-	-	-	-	-	-
LuChry	10	null	-29.02	0	0.7880	NA	NA	NA
		lin	-24.92	4.093	0.1018	0.000289	-0.001073	0.001652
		exp2	-24.87	4.147	0.0991	0.006607	-0.049263	0.089741
		log3	-19.26	9.750	0.0060	0.119522	-	-
		exp3	-18.92	10.093	0.0051	0.000011	-	-
		log4	-	-	-	-	-	-
LuCocc	10	exp3	-32.77	0	0.5614	0.270619	0.117408	0.612481
		exp2	-31.92	0.853	0.3664	0.163376	0.031509	0.423146
		null	-26.92	5.856	0.0300	NA	NA	NA
		lin	-26.51	6.260	0.0245	0.001318	0.000060	0.002576

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
LuCocc		log3	-25.85	6.927	0.0176	0.192553	0.060173	-
(cont.)		log4	-	-	-	-	-	-
LyArde	10	null	-17.27	0	0.7865	NA	NA	NA
		exp2	-13.11	4.164	0.0980	0.002221	-0.011062	0.016976
		lin	-13.09	4.179	0.0973	0.000387	-0.002074	0.002849
		exp3	-9.11	8.160	0.0133	0.288541	-	-
		log3	-7.11	10.168	0.0049	0.002678	-	-
		log4	-	-	-	-	-	-
MiDolo	10	null	-7.48	0	0.5915	NA	NA	NA
		exp2	-5.32	2.164	0.2005	0.006753	-0.002344	0.016894
		lin	-5.17	2.308	0.1865	0.002601	-0.001056	0.006258
		exp3	0.31	7.793	0.0120	0.041476	-	-
		log3	0.78	8.259	0.0095	0.011087	-	-
		log4	-	-	-	-	-	-
MiPunc	9	exp2	-39.24	0	0.8197	0.135850	0.032277	0.375272
		null	-34.98	4.260	0.0974	NA	NA	NA
		lin	-33.94	5.303	0.0578	0.000812	0.000004	0.001620
		log3	-31.98	7.256	0.0218	0.144685	0.037621	-
		log4	-26.96	12.281	0.0018	0.747399	-	9.271917
		exp3	-26.73	12.507	0.0016	-0.000074	-	-
MiSalm	10	exp2	-32.18	0	0.4734	0.024997	0.010259	0.047737
		exp3	-31.59	0.594	0.3517	0.095920	0.032342	0.266168
		lin	-29.11	3.078	0.1016	0.001483	0.000378	0.002589
		null	-27.63	4.550	0.0487	NA	NA	NA
		log3	-25.90	6.284	0.0204	0.027030	0.010316	-
		log4	-22.79	9.398	0.0043	7.552312	-	31.540971
MoCerv	6	null	-24.44	0	0.9165	NA	NA	NA
		lin	-18.26	6.176	0.0418	0.001060	-0.000137	0.002256
		exp2	-18.26	6.181	0.0417	0.061688	-0.007422	0.293693
		exp3	11.66	36.100	0.0000	0.029297	-	-
		log3	11.72	36.164	0.0000	0.077982	-	-
		log4	-	-	-	-	-	-
NoChil	9	lin	-38.58	0	0.6679	0.001819	0.001195	0.002443
		exp2	-36.98	1.604	0.2994	0.026591	0.015491	0.040783
		exp3	-31.37	7.216	0.0181	0.000408	-	0.067159
		log3	-30.31	8.269	0.0107	0.053108	0.017340	0.545068
		null	-28.28	10.307	0.0039	NA	NA	NA
		log4	-18.31	20.269	0.0000	18.829488	-	68.030916
NoCrys	10	null	-52.69	0	0.6066	NA	NA	NA
		exp2	-50.70	1.991	0.2242	-0.034228	-	0.009818
		lin	-49.90	2.785	0.1507	-0.000239	-0.000630	0.000152
		log3	-44.68	8.012	0.0110	-0.034263	-	-
		exp3	-43.90	8.786	0.0075	0.000044	-	-
		log4	-	-	-	-	-	-
NoHuds	8	null	-21.38	0	0.6603	NA	NA	NA
		lin	-18.67	2.714	0.1700	0.001503	-0.000306	0.003313
		exp2	-18.62	2.761	0.1660	0.041193	-0.009427	0.172678

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
NoHuds		log3	-9.87	11.510	0.0021	0.320272	-	-
(cont.)		exp3	-9.40	11.985	0.0016	0.018407	-	-
		log4	8.39	29.776	0.0000	2.550576	-	-
NoInsi	10	exp2	-11.09	0	0.4424	0.016302	0.004794	0.031006
		lin	-10.69	0.406	0.3611	0.003834	0.001058	0.006611
		null	-8.96	2.134	0.1522	NA	NA	NA
		exp3	-5.20	5.893	0.0232	0.030132	-0.107460	-
		log3	-5.00	6.090	0.0211	0.021853	-	-
		log4	-	-	-	-	-	-
NoLept	10	exp3	-4.49	0	0.5072	0.153149	0.048254	0.413541
		exp2	-3.16	1.327	0.2612	0.013176	0.004382	0.023672
		lin	-2.05	2.443	0.1495	0.005803	0.001526	0.010079
		null	-0.48	4.012	0.0682	NA	NA	NA
		log3	4.06	8.551	0.0071	0.023566	-	0.125759
		log4	4.11	8.594	0.0069	2.284276	-	11.385326
NoLeuc	9	exp2	-43.05	0	0.8495	0.142908	0.046012	0.355201
		null	-38.24	4.811	0.0766	NA	NA	NA
		lin	-37.18	5.868	0.0452	0.000676	0.000002	0.001351
		exp3	-36.28	6.777	0.0287	0.167454	0.031963	0.537122
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
NoPhot	10	exp2	-13.83	0	0.5287	-0.020027	-0.031942	-0.010021
		log4	-11.63	2.199	0.1761	2.191661	-7.085648	6.640346
		lin	-11.16	2.672	0.1390	-0.004384	-0.007096	-0.001672
		exp3	-10.74	3.089	0.1129	-0.056569	-0.127568	-0.010314
		null	-7.88	5.946	0.0271	NA	NA	NA
		log3	-6.86	6.968	0.0162	-0.026668	-0.059956	-0.010711
NoPlat	10	null	-12.50	0	0.7753	NA	NA	NA
		exp2	-8.21	4.285	0.0910	0.000094	-0.012684	0.013888
		lin	-8.21	4.286	0.0910	0.000021	-0.003121	0.003163
		exp3	-6.68	5.819	0.0423	0.326663	0.009776	-
		log4	2.23	14.723	0.0005	1.022618	-	-
		log3	-	-	-	-	-	-
NoProc	8	null	-31.16	0	0.8830	NA	NA	NA
		exp2	-25.73	5.436	0.0583	-0.013294	-	-
		lin	-25.71	5.457	0.0577	-0.000197	-0.001363	0.000968
		exp3	-16.41	14.758	0.0006	-0.031326	-	-
		log3	-16.39	14.770	0.0005	-0.013529	-	-
		log4	-	-	-	-	-	-
NoRube	10	null	-8.07	0	0.4788	NA	NA	NA
		exp2	-6.62	1.446	0.2324	-0.012473	-0.029485	0.001885
		lin	-5.92	2.145	0.1638	-0.002618	-0.006141	0.000905
		exp3	-5.19	2.873	0.1139	-0.142595	-	-0.017729
		log3	-0.31	7.753	0.0099	-0.015594	-	-
		log4	3.80	11.862	0.0013	5.502790	-69.079195	-
NoRubr	9	exp2	-15.04	0	0.5877	0.038743	0.018601	0.076536
		lin	-14.03	1.017	0.3535	0.004954	0.002512	0.007396

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
NoRubr		null	-8.61	6.429	0.0236	NA	NA	NA
(cont.)		exp3	-8.49	6.555	0.0222	0.120586	-0.073476	0.588717
		log3	-7.41	7.630	0.0130	0.044728	0.019072	0.157576
		log4	3.72	18.767	0.0000	5.401597	-	54.797258
NoScab	10	null	-14.07	0	0.5790	NA	NA	NA
		exp2	-11.99	2.079	0.2048	-0.008613	-0.020872	0.002869
		lin	-11.52	2.545	0.1622	-0.001766	-0.004428	0.000897
		exp3	-8.92	5.150	0.0441	-0.089955	-	-
		log3	-5.82	8.253	0.0093	-0.010798	-	-
		log4	-0.33	13.734	0.0006	4.841918	-	-
NoTele	10	lin	-24.37	0	0.5169	0.003220	0.001819	0.004621
		exp2	-23.96	0.406	0.4220	0.024356	0.012643	0.040052
		exp3	-18.39	5.976	0.0260	0.004586	-0.081634	0.090023
		log3	-18.17	6.197	0.0233	0.037898	0.016696	0.147741
		null	-16.76	7.603	0.0115	NA	NA	NA
		log4	-8.96	15.405	0.0002	3.555030	-	-
NoVolu	10	null	-25.81	0	0.7938	NA	NA	NA
		exp2	-21.54	4.263	0.0942	0.001407	-0.018843	0.024545
		lin	-21.54	4.268	0.0939	0.000102	-0.001512	0.001716
		exp3	-17.63	8.173	0.0133	0.305801	-	-
		log3	-15.54	10.263	0.0047	0.001503	-	-
		log4	-	-	-	-	-	-
OnMyki	10	exp2	-15.95	0	0.5794	0.025199	0.013388	0.041940
		lin	-14.40	1.551	0.2669	0.004820	0.002514	0.007126
		exp3	-12.81	3.136	0.1208	0.136565	0.004742	0.424075
		log3	-9.26	6.689	0.0204	0.031379	0.015050	0.109098
		null	-8.08	7.872	0.0113	NA	NA	NA
		log4	-3.61	12.334	0.0012	5.233282	-	47.991126
PeCapr	5	null	-17.38	0	0.9999	NA	NA	NA
		exp2	2.49	19.865	0.0000	-0.024812	-	-
		lin	2.49	19.868	0.0000	-0.000356	-0.003321	0.002608
		log4	-	-	-	-	-	-
		exp3	-	-	-	0.000682	-	-
		log3	-	-	-	-0.044270	-	-
PeFlav	10	null	-62.24	0	0.7094	NA	NA	NA
		exp2	-59.09	3.154	0.1465	-0.022524	-	0.026878
		lin	-58.85	3.389	0.1303	-0.000116	-0.000366	0.000133
		log3	-53.09	9.157	0.0073	-0.022624	-	-
		exp3	-52.85	9.389	0.0065	0.000017	-	-
		log4	-	-	-	-	-	-
PeGymn	10	exp2	-23.13	0	0.4498	0.011862	0.003703	0.021285
		lin	-22.13	1.008	0.2717	0.002068	0.000501	0.003635
		null	-20.80	2.334	0.1400	NA	NA	NA
		exp3	-20.45	2.684	0.1175	0.103170	0.001674	0.594261
		log3	-16.89	6.246	0.0198	0.014485	-	-
		log4	-11.34	11.789	0.0012	8.744484	-	128.929252
PeOxyr	10	lin	-36.14	0	0.3525	-0.000867	-0.001644	-0.000089

<div align="center">-continued-</div>

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
PeOxyr		null	-36.13	0.013	0.3503	NA	NA	NA
(cont.)		exp2	-35.46	0.687	0.2501	-0.013931	-0.030035	-0.000044
		log3	-31.19	4.950	0.0297	-0.094948	-	-
		exp3	-30.14	6.002	0.0175	-0.000048	-	-
		log4	-	-	-	-	-	-
PeRoan	8	lin	-27.23	0	0.4701	0.001875	0.000816	0.002934
		exp2	-27.01	0.222	0.4206	0.038615	0.014851	0.076563
		null	-24.12	3.113	0.0992	NA	NA	NA
		log3	-18.28	8.955	0.0053	0.076816	-	-
		exp3	-18.05	9.189	0.0048	0.015240	-0.173272	0.154994
		log4	-	-	-	-	-	-
PhTere	10	null	-17.74	0	0.5433	NA	NA	NA
		exp2	-15.91	1.836	0.2170	-0.006771	-0.015523	0.001712
		lin	-15.54	2.199	0.1809	-0.001595	-0.003773	0.000582
		exp3	-12.89	4.849	0.0481	-0.090677	-	0.016685
		log3	-9.76	7.982	0.0100	-0.008838	-	-
		log4	-4.34	13.400	0.0007	4.144330	-	-
PiNota	10	null	-11.53	0	0.6594	NA	NA	NA
		exp2	-8.30	3.229	0.1312	-0.007081	-0.022446	0.007205
		lin	-8.03	3.495	0.1149	-0.001383	-0.004553	0.001787
		exp3	-7.51	4.018	0.0884	-0.146992	-	-0.026065
		log3	-2.19	9.342	0.0062	-0.008579	-	-
		log4	-	-	-	-	-	-
PiProm	6	null	-23.60	0	0.9466	NA	NA	NA
		lin	-16.83	6.770	0.0321	0.001068	-0.000280	0.002416
		exp2	-16.02	7.587	0.0213	0.037278	-0.019505	0.152879
		log3	11.91	35.512	0.0000	0.924200	-	-
		exp3	13.17	36.775	0.0000	0.000275	-	-
		log4	-	-	-	1.082016	-	-
PoAnnu	10	null	-65.08	0	0.6284	NA	NA	NA
		lin	-62.91	2.174	0.2119	-0.000150	-0.000354	0.000054
		exp2	-62.21	2.876	0.1492	-0.025946	-	-
		exp3	-56.91	8.175	0.0105	-0.000058	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-
PoNigr	8	null	-44.12	0	0.8841	NA	NA	NA
		exp2	-38.67	5.445	0.0581	0.021476	-	-
		lin	-38.62	5.496	0.0566	0.000075	-0.000445	0.000595
		exp3	-29.53	14.591	0.0006	0.111588	-	-
		log3	-29.34	14.779	0.0005	0.021537	-	-
		log4	-	-	-	-	-	-
RhAtra	10	null	-13.46	0	0.7903	NA	NA	NA
		exp2	-9.18	4.280	0.0930	0.000175	-0.004623	0.005087
		lin	-9.18	4.280	0.0930	0.000106	-0.002888	0.003100
		exp3	-6.45	7.007	0.0238	0.329104	-	-
		log3	-	-	-	-	-	-
		log4	-	-	-	-	-	-

-continued-

Species	n	Model	AICc	Δ_i	w_i	β_1	β_1 LCL	β_1 UCL
RhCata	10	null	-10.17	0	0.7561	NA	NA	NA
		exp2	-6.12	4.046	0.1000	0.002013	-0.006438	0.011027
		lin	-6.10	4.074	0.0986	0.000777	-0.002715	0.004269
		exp3	-4.31	5.857	0.0404	0.261477	-0.001868	-
		log3	-0.10	10.069	0.0049	0.003239	-	-
		log4	-	-	-	-	-	-
SaFont	10	null	-13.95	0	0.7526	NA	NA	NA
		lin	-10.16	3.788	0.1132	0.000979	-0.001871	0.003829
		exp2	-10.08	3.873	0.1085	0.004463	-0.009909	0.021051
		log3	-6.69	7.257	0.0200	0.190825	-	-
		exp3	-4.16	9.789	0.0056	0.000018	-	-
		log4	-	-	-	-	-	-
SaTrut	10	exp2	-25.75	0	0.8479	0.044405	0.031879	0.062017
		lin	-21.15	4.603	0.0849	0.006008	0.004363	0.007653
		exp3	-19.78	5.976	0.0427	0.041440	0.002495	0.104339
		log3	-18.63	7.121	0.0241	0.054264	0.036839	0.092995
		log4	-9.63	16.118	0.0003	18.064207	7.122316	25.487890
		null	-6.32	19.432	0.0001	NA	NA	NA
SeAtro	10	null	-12.00	0	0.7486	NA	NA	NA
		exp2	-8.39	3.603	0.1236	-0.003969	-0.014009	0.006074
		lin	-8.27	3.728	0.1161	-0.001141	-0.004274	0.001992
		log3	-2.32	9.675	0.0059	-0.005489	-	-
		exp3	-2.27	9.728	0.0058	0.000015	-	-
		log4	-	-	-	-	-	-
ThRhot	10	exp2	-46.02	0	0.5743	0.217318	0.020081	-
		exp3	-44.00	2.022	0.2090	0.260544	0.098499	-
		null	-42.31	3.712	0.0898	NA	NA	NA
		lin	-41.90	4.127	0.0729	0.000610	0.000027	0.001193
		log3	-41.30	4.728	0.0540	0.503067	-	-
		log4	-	-	-	-	-	-

Table S4 Data used for classification tree analysis of the form of spread observed for 39 introduced upper and middle New River tributary fishes. The response variable was *Form* and explanatory variables were *GensSinceDetect*, *CPUE1*, and *IntroEffort*. Species codes are defined in Table 2.1.

Species	Form	t	GenTime	GensSinceDetect	CPUE1	IntroEffort
AmCalv	Sta	61	5.664	10.770	0	1
AmMela	Sta	75	3.419	21.934	0	1
AmNata	Sta	38	3.467	10.961	0	1
AmNebu	Exp	38	4.099	9.270	0	1
AmRupe	Exp	139	6.224	22.331	0.321	3
CaAura	Sta	24	2.206	10.880	0	2
CyCarp	Sta	129	5.520	23.368	0	3
CyGala	Exp	60	2.881	20.830	0	2
EsNige	Sta	61	2.963	20.590	0.018	2
EtCaer	Exp	42	0.622	67.570	0	1
EtOlms	Exp	28	0.957	29.266	0	1
EtSimo	Lin	38	0.677	56.131	0	2
ExMaxi	Exp	58	2.375	24.426	0	2
LeAuri	Exp	75	2.775	27.026	0.125	3
LeGibb	Sta	94	2.892	32.507	0.018	3
LeMacr	Sta	78	2.676	29.152	0.125	3
LeMega	Sta	86	1.826	47.088	0	1
LeMicr	Sta	22	2.120	10.379	0	3
LuCera	Exp	63	2.331	27.025	0.107	2
LuCocc	Exp	73	1.890	38.627	0.036	2
MiDolo	Sta	136	7.136	19.060	0.321	3
MiPunc	Exp	86	2.958	29.071	0	3
MiSalm	Exp	86	7.282	11.810	0.089	3
MoCerv	Sta	27	2.202	12.262	0	1
NoChil	Lin	51	0.658	77.488	0	2
NoCrys	Sta	65	4.461	14.570	0.036	3
NoHuds	Sta	66	1.931	34.171	0	1
NoLeuc	Exp	51	1.478	34.516	0	1
NoProc	Sta	43	1.149	37.429	0	1
NoRubr	Exp	51	1.691	30.162	0	2
NoTele	Lin	56	0.853	65.655	0	2
OnMyki	Exp	134	1.939	69.100	0.071	3
PeFlav	Sta	97	2.961	32.765	0.018	3
PeRoan	Lin	51	0.913	55.869	0	1
PiProm	Sta	56	1.422	39.374	0	2
PoAnnu	Sta	62	3.958	15.663	0	3
PoNigr	Sta	65	5.874	11.065	0	3
SaTrut	Exp	52	6.168	8.430	0	3
ThRhot	Exp	23	2.720	8.457	0.018	1

Table S5 List of compiled fish traits and introduction attributes and their derivation.

Domain	Trait	Description	Data type	Derivation
		Biological traits		
LIFE HISTORY	AGE1REPRO	Typical age at first reproduction (years)	numeric	Jenkins & Burkhead (1994)
	LEN1REPRO	Lower limit of typical adult length range (total length, mm)	numeric	
	FECUNDITY	Maximum reported fecundity (egg count)	numeric	Frimpong & Angermeier (2009)
	LONGEVITY	Longevity based on life in the wild (years)	numeric	
	GENTIME	Average age of parents at the time their young are born.	numeric	Estimated from MAXTL, LEN1REPRO, AGE1REPRO according to equations of Froese & Binohlan (2000)
	PERIOD_D	Distance in multivariate trait space between each species' position and Winemiller & Rose (1992) life history end-point. Smaller distances indicate greater affiliation with a given end-point.	numeric	Euclidean distances (scaled to unit variance) determined by McManamay & Frimpong (2015)
	EQUIL_D		numeric	
	OPPORT_D		numeric	
MORPHOLOGY	MAXTL	Maximum total length (mm) reported from Virginia where available; otherwise a record from a neighboring state was accepted	numeric	Frimpong & Angermeier (2009) and Frimpong lab's New River fish collections (described in Chapter 2).
	MTHANG	Mandible angle on a scale from -1 (inferior) to +1 (superior)	numeric	Measured from a photo of a representative adult female. Photos from Jenkins & Burkhead (1994) were used when available.
	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	Based on Balon's (1975) reproductive guilds as assigned by Frimpong & Angermeier (2009). *Nocomis* nest associates assigned by Pendleton et al. (2012).
	SEASON	Length of spawning season (months, precision = 0.25)	numeric	Frimpong & Angermeier (2009)
	SERIAL	Serial/batch spawner	binary	
	TIMING	Spawning starts in (1) Apr–Sept vs. (0) Oct–Mar.	binary	
	TSPAWNMIN	Minimum spawning temperature (C)	numeric	Simon & Wallus (1990–2008) if available, otherwise Jenkins & Burkhead (1994) or Etnier & Starnes (1993)
PHYSI-OLOGY	TMIN_JAN	Average minimum January air temperature (C) at native range centroid	numeric	10-minute resolution GIS grid of monthly global air temperature averages downloaded from worldclim.org (Hijmans *et al.,* 2005).
	TMAX_JUL	Average maximum July air temperature (C) at range centroid	numeric	
		Ecological traits		
GEOGRA-PHIC DISTRIB-UTION	AREAKM2	Size of native range (km^2)	numeric	Range maps of Page & Burr (1991) as georeferenced by Frimpong & Angermeier (2009)
	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	

-continued-

Domain	Trait	Description	Data type	Derivation
		Ecological traits (cont.)		
HABITAT PREFERENCE	PREFLOT	Prefers lotic systems	binary	Frimpong & Angermeier (2009)
	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	Sum of the following physiographic traits of Frimpong & Angermeier (2009): LOWLAND, UPLAND, and MONTANE
	WATBRE	Total number of preferred waterbody types	ordinal	Sum of the following waterbody-type traits of Frimpong & Angermeier (2009): LARGERIV, SMALLRIV, CREEK, SPRGSUBT, LACUSTRINE
	LITHOPHIL	Rock, gravel, or sand spawner	binary	LITHOPHIL = 1 if any of the following Balon reproductive guilds were assigned by Frimpong & Angermeier (2009): A.1.3A; A.1.3B; A.2.3A; A.2.3B; B.1.3A; B.2.3A; or B.2.3B
TROPHIC	BENTHIC	Benthic feeder	binary	All trophic classes as assigned by Frimpong & Angermeier (2009). The given item forms a significant component (>5%) of the adult diet
	SURWCOL	Surface or water column feeder	binary	
	ALGPHYTO	Algae or phytoplankton	binary	
	FSHCRCRB	Fishes, crayfishes, crabs, frogs	binary	
	EGGS	Eggs of fishes, frogs, etc.	binary	
		Introduction attributes		
INTRODUCTION CONTEXT	FIRSTREC	Year species was first detected in the New River drainage	numeric	Table S1 in Chapter 2
	INTROEFF	Introduction effort: estimated total number of individuals released in the New River drainage since European settlement: (1) <100; (2) 100–1000; (3) >1,000.	ordinal	Table S4 in Chapter 2
	GAME	Usually used by humans as gamefish, baitfish, or commercially	binary	Primary source was Froese & Pauly (2015). Uses in the study region corroborated by Jenkins & Burkhead (1994)

	Trait	Description	Data type	Correlated with
		Correlated species traits and introduction attributes excluded from analyses		
	T_TOL	Temperature tolerance: TMAX_JUL - TMIN_JAN	numeric	TMIN_JAN (Pearson's r = -0.856)
	BENINV	Benthic invertivore: INVLVFSH=1 & BENTHIC = 1 & SURWCOL = 0) (Frimpong & Angermeier, 2009)	binary	SURWCOL (r = -1)
	HERB	Herbivore: ALGPHYTO = 1 or MACVASCU = 1 or DETRITUS = 1 (Frimpong & Angeremeir, 2009)	binary	ALGPHYTO (r = 0.850)
	DIETBRE	Diet breadth: sum of FishTraits binary (0, 1) trophic classes ALGPHYTO, MACVASCU, DETRITUS, INVLVFSH, FSHCRCRB, BLOOD, EGGS, OTHER (Frimpong & Angermeier, 2009)	ordinal	ALGPHYTO (r = 0.733) and HERB (Spearman's ρ = 0.827)
	LATRANGE	Latitudinal range of native range: LATMAX - LATMIN (Frimpong & Angermeier, 2009)	numeric	AREAKM2 (r = 0.903)
	DNAT	Distance from nearest native source (introduced species only)	numeric	LONCEN (r = 0.910)

Table S6 Phylogenetic distance matrix (**D**). Pairwise distances represent the number of nodes between genera on a phylogenetic tree based on Betancur et al. (2013), with lower levels (order/family to genus) compiled from various sources listed in *Methods*.

Species code	AmCalv	DoCepe	DoPete	EsNige	CyCarp	CaAura	NoCrys	ExMaxi	HyHyps	CyGala	LuCocc	LuCera	NoLeuc	NoRubr	NoChil	NoTele	NoHuds	NoProc	PiProm	ThRhot	MoCerv
AmCalv	0																				
DoCepe	17	0																			
DoPete	17	0	0																		
EsNige	13	21	21	0																	
CyCarp	22	28	28	26	0																
CaAura	20	26	26	24	5	0															
NoCrys	21	27	27	25	22	20	0														
ExMaxi	24	30	30	28	25	23	10	0													
HyHyps	30	36	36	34	31	29	16	11	0												
CyGala	32	38	38	36	33	31	18	13	3	0											
LuCocc	32	38	38	36	33	31	18	13	3	3	0										
LuCera	29	35	35	33	30	28	15	10	4	6	6	0									
NoLeuc	30	36	36	34	31	29	16	11	3	5	5	4	0								
NoRubr	30	36	36	34	31	29	16	11	3	5	5	4	0	0							
NoChil	30	36	36	34	31	29	16	11	3	5	5	4	0	0	0						
NoTele	27	33	33	31	28	26	13	8	4	6	6	3	4	4	4	0					
NoHuds	27	33	33	31	28	26	13	8	4	6	6	3	4	4	4	0	0				
NoProc	30	36	36	34	31	29	16	11	3	5	5	4	0	0	0	4	4	0			
PiProm	32	38	38	36	33	31	18	13	5	7	7	6	3	3	3	6	6	3	0		
ThRhot	17	23	23	21	20	18	19	22	28	30	30	27	28	28	28	25	25	28	30	0	
MoCerv	17	23	23	21	20	18	19	22	28	30	30	27	28	28	28	25	25	28	30	3	0
AmNata	14	20	20	18	19	17	18	21	27	29	29	26	27	27	27	24	24	27	29	14	14
AmNebu	14	20	20	18	19	17	18	21	27	29	29	26	27	27	27	24	24	27	29	14	14
AmMela	14	20	20	18	19	17	18	21	27	29	29	26	27	27	27	24	24	27	29	14	14
SaTrut	13	21	21	7	26	24	25	28	34	36	36	33	34	34	34	31	31	34	36	21	21
OnMyki	14	22	22	8	27	25	26	29	35	37	37	34	35	35	35	32	32	35	37	22	22
AmRupe	26	34	34	28	39	37	38	41	47	49	49	46	47	47	47	44	44	47	49	34	34
PoNigr	27	35	35	29	40	38	39	42	48	50	50	47	48	48	48	45	45	48	50	35	35
PoAnnu	27	35	35	29	40	38	39	42	48	50	50	47	48	48	48	45	45	48	50	35	35
MiDolo	22	30	30	24	35	33	34	37	43	45	45	42	43	43	43	40	40	43	45	30	30
MiPunc	22	30	30	24	35	33	34	37	43	45	45	42	43	43	43	40	40	43	45	30	30
MiSalm	22	30	30	24	35	33	34	37	43	45	45	42	43	43	43	40	40	43	45	30	30
LeAuri	21	29	29	23	34	32	33	36	42	44	44	41	42	42	42	39	39	42	44	29	29
LeMega	21	29	29	23	34	32	33	36	42	44	44	41	42	42	42	39	39	42	44	29	29
LeMacr	21	29	29	23	34	32	33	36	42	44	44	41	42	42	42	39	39	42	44	29	29
LeGibb	21	29	29	23	34	32	33	36	42	44	44	41	42	42	42	39	39	42	44	29	29
LeMicr	21	29	29	23	34	32	33	36	42	44	44	41	42	42	42	39	39	42	44	29	29
PeFlav	22	30	30	25	35	33	34	37	43	45	45	42	43	43	43	40	40	43	45	30	30
PeRoan	25	33	33	27	38	36	37	40	46	48	48	45	46	46	46	43	43	46	48	33	33
EtSimo	25	33	33	27	38	36	37	40	46	48	48	45	46	46	46	43	43	46	48	33	33
EtOlms	25	33	33	27	38	36	37	40	46	48	48	45	46	46	46	43	43	46	48	33	33
EtCaer	25	33	33	27	38	36	37	40	46	48	48	45	46	46	46	43	43	46	48	33	33

-continued-

Species code	AmCalv	DoCepe	DoPete	EsNige	CyCarp	CaAura	NoCrys	ExMaxi	HyHyps	CyGala	LuCocc	LuCera	NoLeuc	NoRubr	NoChil	NoTele	NoHuds	NoProc	PiProm	ThRhot	MoCerv
AmNata	0																				
AmNebu	0	0																			
AmMela	0	0	0																		
SaTrut	18	18	18	0																	
OnMyki	19	19	19	2	0																
AmRupe	31	31	31	28	29	0															
PoNigr	32	32	32	29	30	2	0														
PoAnnu	32	32	32	29	30	2	0	0													
MiDolo	27	27	27	24	25	5	6	6	0												
MiPunc	27	27	27	24	25	5	6	6	0	0											
MiSalm	27	27	27	24	25	5	6	6	0	0	0										
LeAuri	26	26	26	23	24	6	7	7	2	2	2	0									
LeMega	26	26	26	23	24	6	7	7	2	2	2	0	0								
LeMacr	26	26	26	23	24	6	7	7	2	2	2	0	0	0							
LeGibb	26	26	26	23	24	6	7	7	2	2	2	0	0	0	0						
LeMicr	26	26	26	23	24	6	7	7	2	2	2	0	0	0	0	0					
PeFlav	27	27	27	25	26	13	14	14	9	9	9	8	8	8	8	8	0				
PeRoan	30	30	30	27	28	16	17	17	12	12	12	11	11	11	11	11	4	0			
EtSimo	30	30	30	27	28	16	17	17	12	12	12	11	11	11	11	11	4	1	0		
EtOlms	30	30	30	27	28	16	17	17	12	12	12	11	11	11	11	11	4	1	0	0	
EtCaer	30	30	30	27	28	16	17	17	12	12	12	11	11	11	11	11	4	1	0	0	0

AmRupe = *Ambloplites rupestris* (rock bass); AmMela = *Ameiurus melas* (black bullhead); AmNata = *A. natalis* (yellow bullhead); AmNebu = *A. nebulosus* (brown bullhead); AmCalv = *Amia calva* (bowfin); CaAnom = *Campostoma anomalum* (central stoneroller); CaAura = *Carassius auratus* (goldfish); CaComm = *Catostomus commersonii* (white sucker); ChOrea = *Chrosomus oreas* (mountain redbelly dace); ClFund = *Clinostomus funduloides* (rosyside dace); CoBair = *Cottus bairdii* (mottled sculpin); CoKana = *C. kanawhae* (Kanawha sculpin); CyGala = *Cyprinella galactura* (whitetail shiner); CySpil = *C. spiloptera* (spotfin shiner); CyCarp = *Cyprinus carpio* (common carp); EsNige = *Esox niger* (chain pickerel); EtBlen = *Etheostoma blennioides* (greenside darter); EtCaer = *E. caeruleum* (rainbow darter); EtFlab = *E. flabellare* (fantail darter); EtKana = *E. kanawhae* (Kanawha darter); EtNigr = *E. nigrum* (Johnny darter); EtOlms = *E. olmstedi* (tessellated darter); EtOsbu = *E. osburni* (candy darter); EtSimo = *E. simoterum* (snubnose darter); ExLaur = *Exoglossum laurae* (tonguetied minnow); ExMaxi = *E. maxillingua* (cutlips minnow); HyNigr = *Hypentelium nigricans* (Northern hogsucker); IcPunc = *Ictalurus punctatus* (channel catfish); LeAuri = *Lepomis auritus* (redbreast sunfish); LeCyan = *L. cyanellus* (green sunfish); LeGibb = *L. gibbosus* (pumpkinseed); LeMacr = *L. macrochirus* (bluegill); LeMega = *L. megalotis* (longear sunfish); LeMicr = *L. microlophus* (redear sunfish); LuAlbe = *Luxilus albeolus* (white shiner); LuCera = *L. cerasinus* (crescent shiner); LuChry = *L. chrysocephalus* (striped shiner); LuCocc = *L. coccogenis* (warpaint shiner); LyArde = *Lythrurus ardens* (rosefin shiner); MiDolo = *Micropterus dolomieu* (smallmouth bass); MiPunc = *M. punctulatus* (spotted bass); MiSalm = *M. salmoides* (largemouth bass); MoCerv = *Moxostoma cervinum* (blacktip jumprock); NoLept = *Nocomis leptocephalus* (bluehead chub); NoPlat = *N. platyrhynchus* (bigmouth chub); NoCrys = *Notemigonus crysoleucas* (golden shiner); NoChil = *Notropis chiliticus* (redlip shiner); NoHuds = *N. hudsonius* (spottail shiner); NoLeuc = *N. leuciodus* (Tennessee shiner); NoPhot = *N. photogenis* (silver shiner); NoProc = *N. procne* (swallowtail shiner); NoRube = *N. rubellus* (rosyface shiner); NoRubr = *N. rubricroceus* (saffron shiner); NoScab = *N. scabriceps* (New River shiner); NoTele = *N. telescopus* (telescope shiner); NoVolu = *N. volucellus* (mimic shiner); NoInsi = *Noturus insignis* (margined madtom); OnMyki = *Oncorhynchus mykiss* (rainbow trout); PeFlav = *Perca flavescens* (yellow perch); PeCapr = *Percina caprodes* (logperch); PeGymn = *P. gymnocephala* (Appalachia darter); PeOxyr = *P. oxyrhynchus* (sharpnose darter); PeRoan = *P. roanoka* (Roanoke darter); PhTere = *Phenacobius teretulus* (Kanawha minnow); PiNota = *Pimephales notatus* (bluntnose minnow); PiProm = *P. promelas* (fathead minnow); PoAnnu = *Pomoxis annularis* (white crappie); PoNigr = *P. nigromaculatus* (black crappie); RhAtra = *Rhinichthys atratulus* (blacknose dace); RhCata = *R. cataractae* (longnose dace); SaTrut = *Salmo trutta* (brown trout); SaFont = *Salvelinus fontinalis* (brook trout); SeAtro = *Semotilus atromaculatus* (creek chub); ThRhot = *Thoburnia rhothoeca* (torrent sucker).
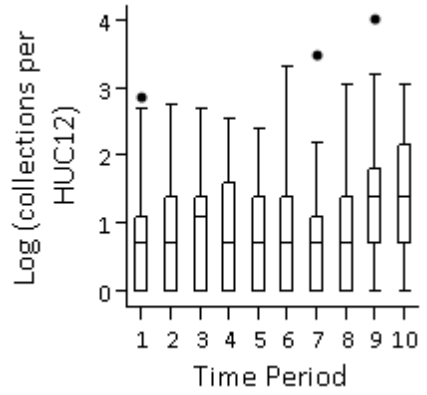
Fig. S1 Box plots of log (number of fish collections per HUC12) for time periods 1–10. The horizontal line within the box represents the median. The lower and upper ends of the box represent the 1st and 3rd quartiles. The whiskers extend to the outermost data point that falls within 1.5 × (interquartile range) of the 1st and 3rd quartiles. A dot indicates an outlier.

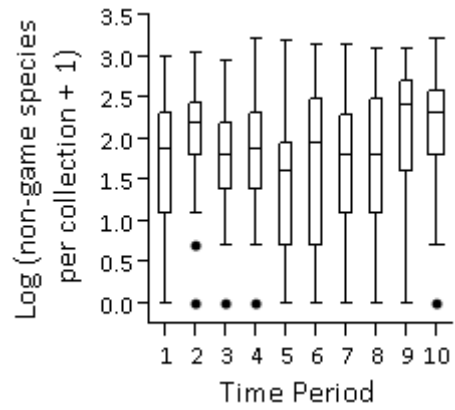**Fig. S2** Box plots of log (number of non-game species reported per collection +1) for time periods 1–10. Box plots were constructed as described in the Fig. S1 caption.

Period 1 (1938–1953) Period 2 (1951–1962) Period 3 (1963–1969)

Period 4 (1970–1976) Period 5 (1977–1983)

N

0   25 mi

0   40 km
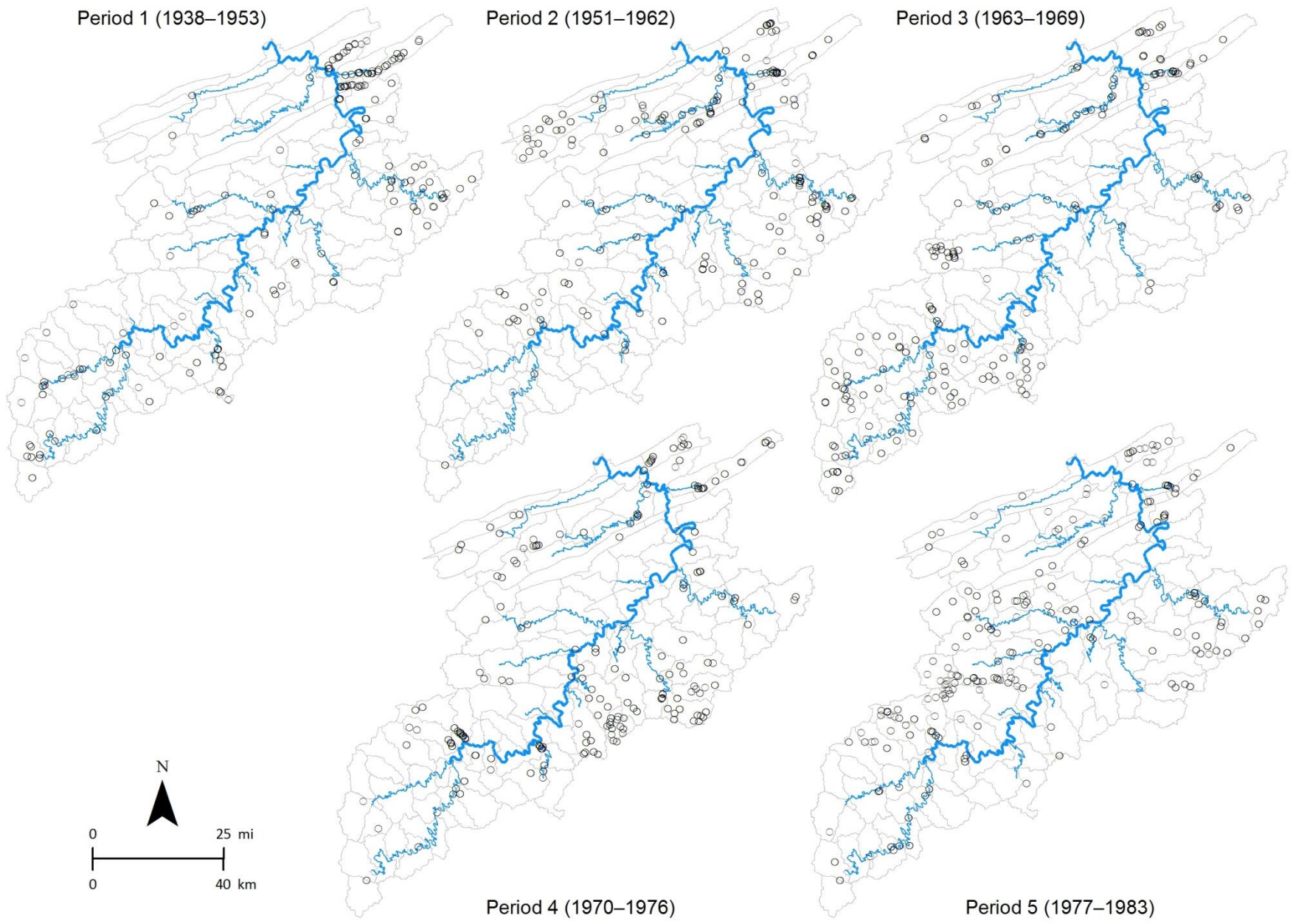
Fig. S3 Time-series maps showing spatial distribution of upper and middle New River fish-collection sites per time period. Page 1 of 2.

Period 6 (1984–1996) Period 7 (1997–1998) Period 8 (1999–2007)

Period 9 (2008–2011) Period 10 (2012–2014)

N

0 25 mi

0 40 km
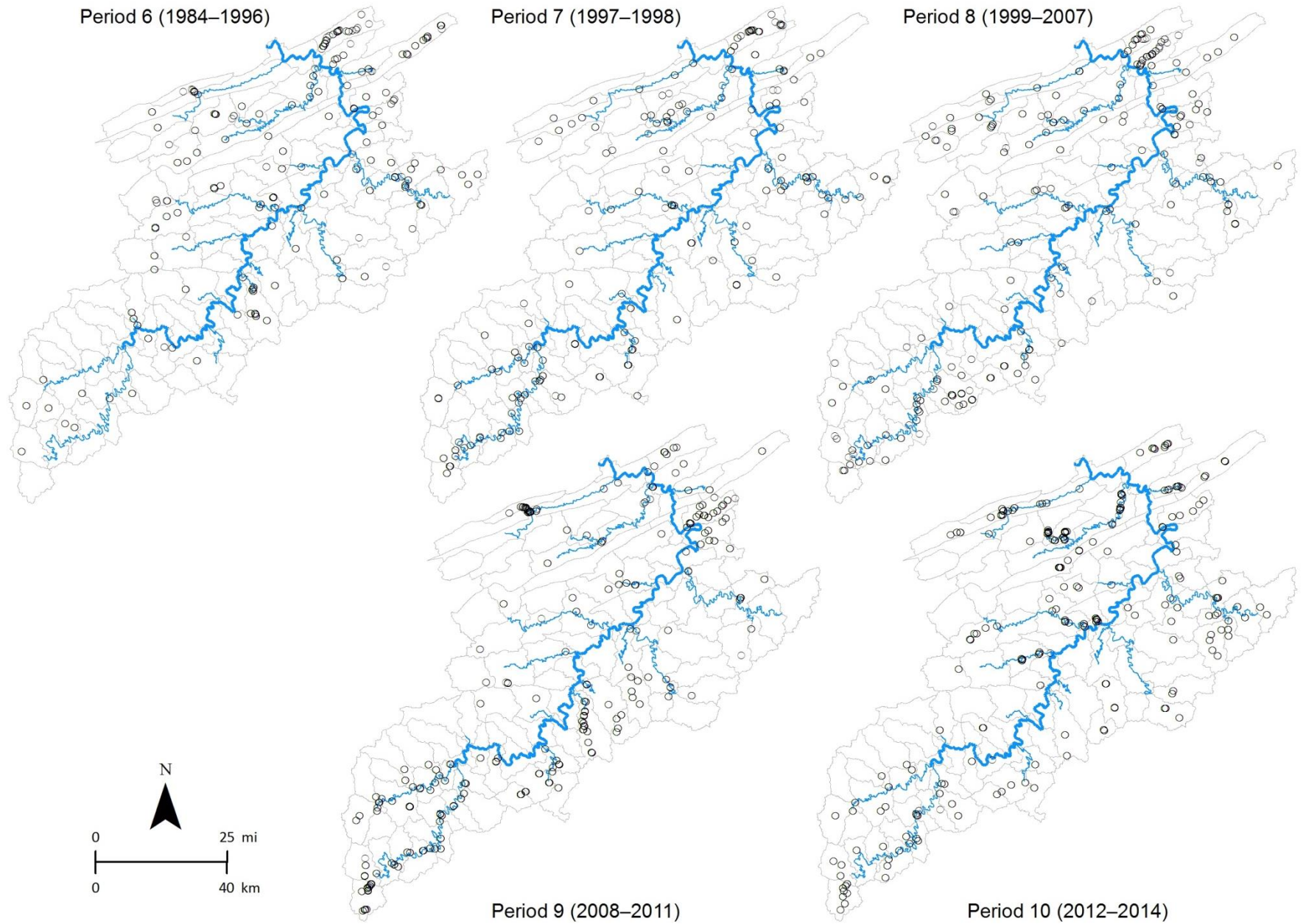
Fig. S3 Page 2 of 2.
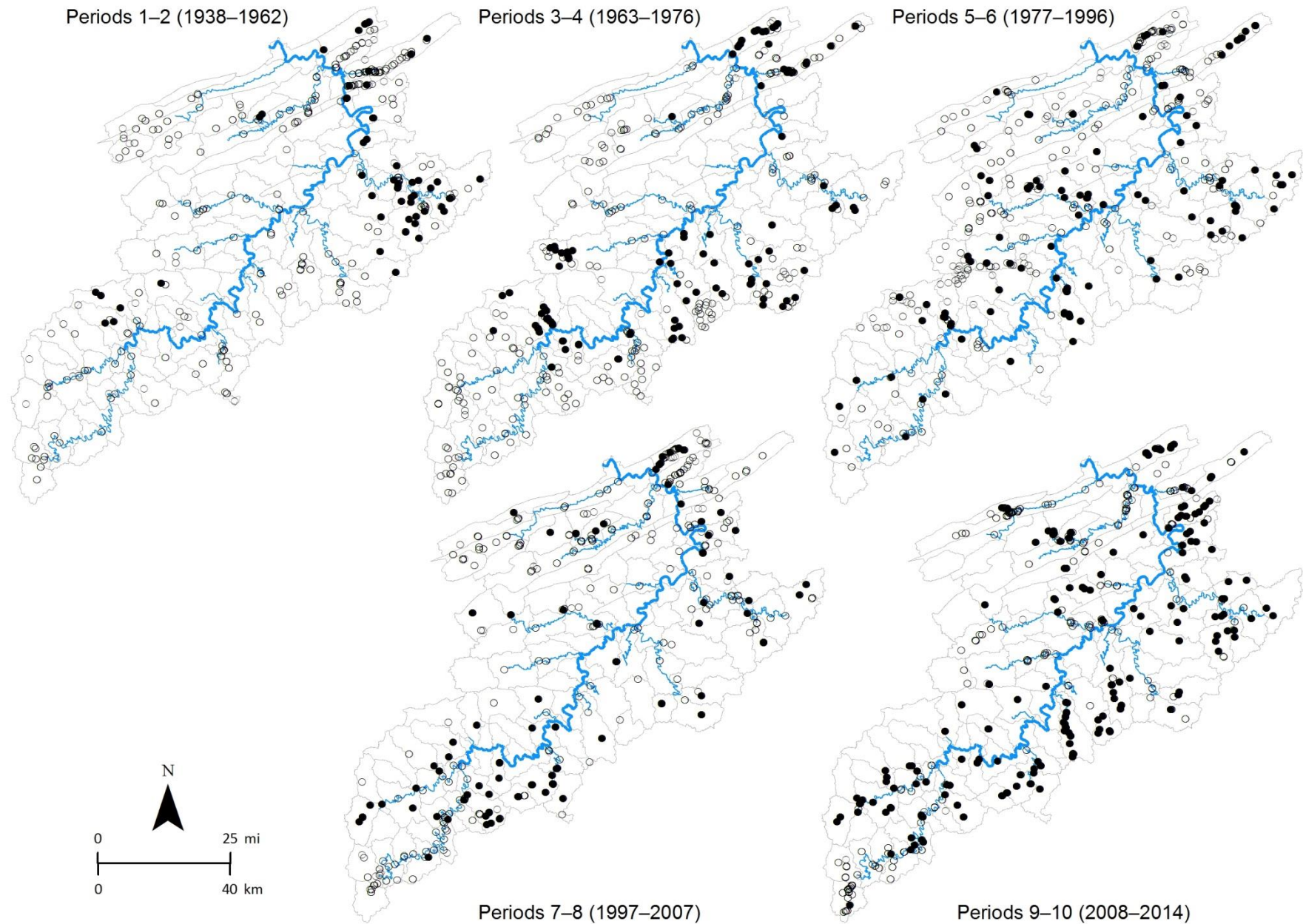
Fig. S4 Time-series maps of mountain redbelly dace *Chrosomus oreas* (strong spreader) occurrence in upper and middle New River tributaries. A solid dot indicates *C. oreas* was collected. A hollow dot indicates a collection from which *C. oreas* was not reported. HUC12 boundaries and the New River mainstem and major tributaries are shown.

Periods 1–2 (1938–1962)

Periods 3–4 (1963–1976)

Periods 5–6 (1977–1996)

Periods 7–8 (1997–2007)

Periods 9–10 (2008–2014)

N

0   25 mi

0   40 km
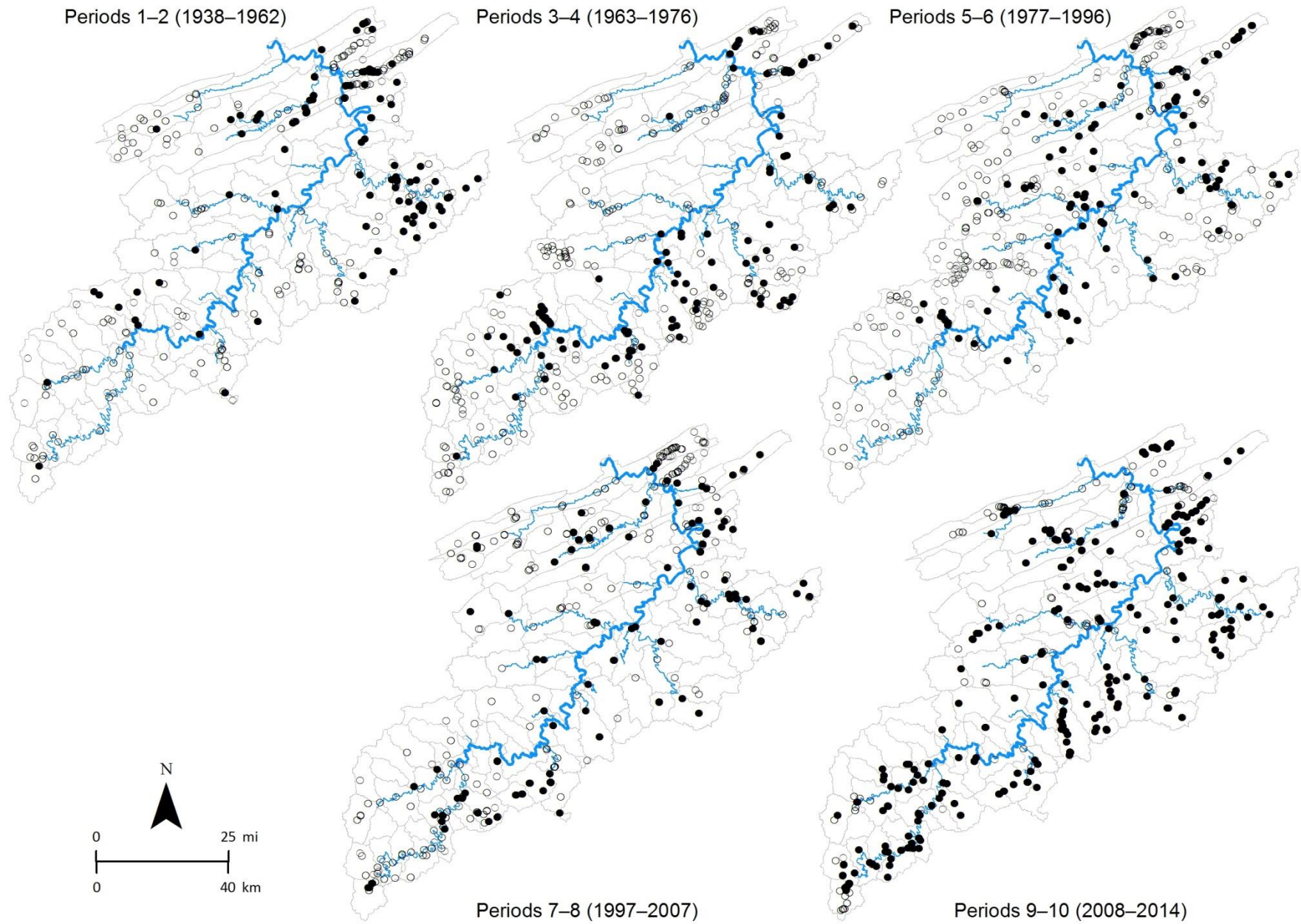
Fig. S5 Time-series maps of bluehead chub *Nocomis leptocephalus* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
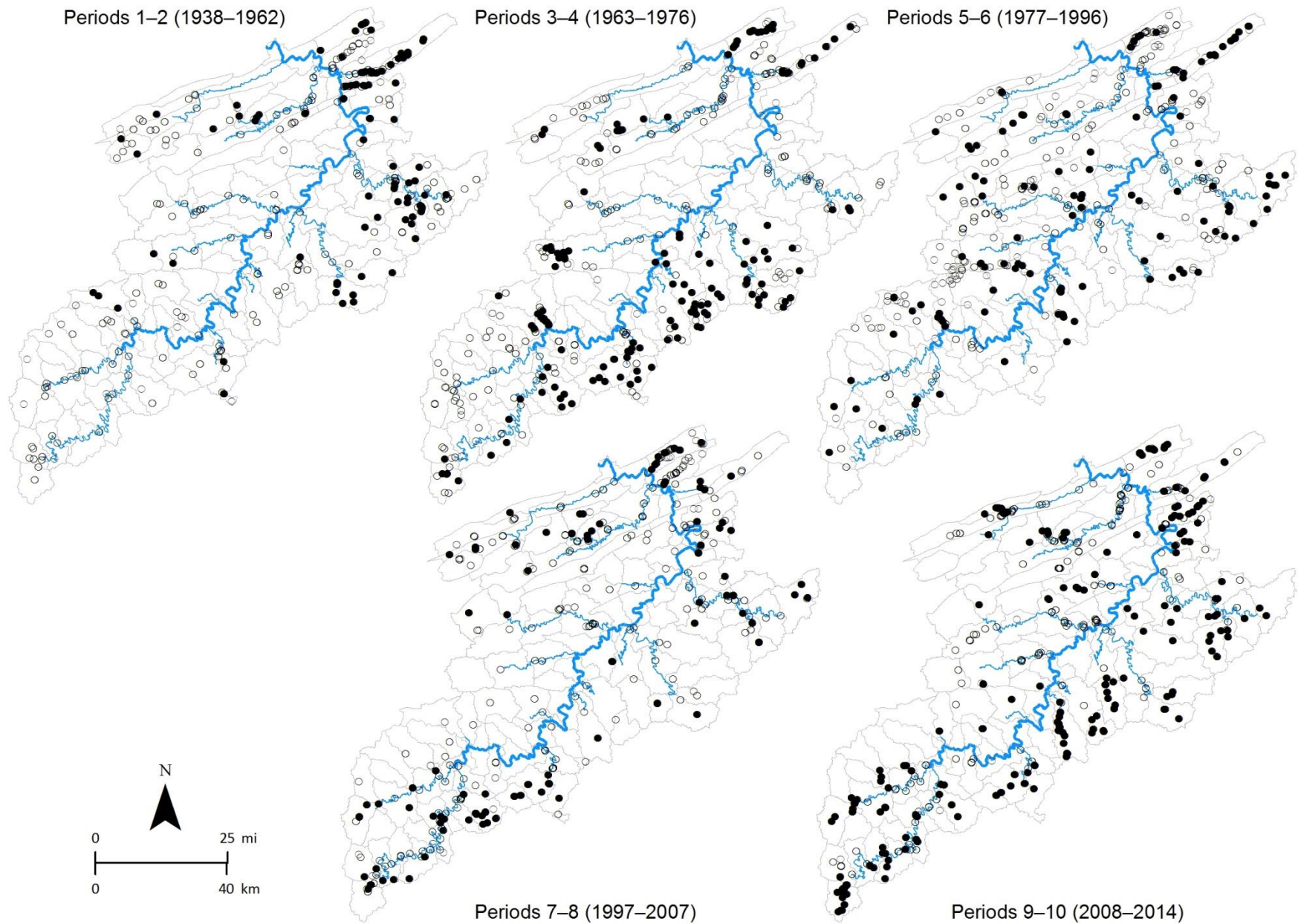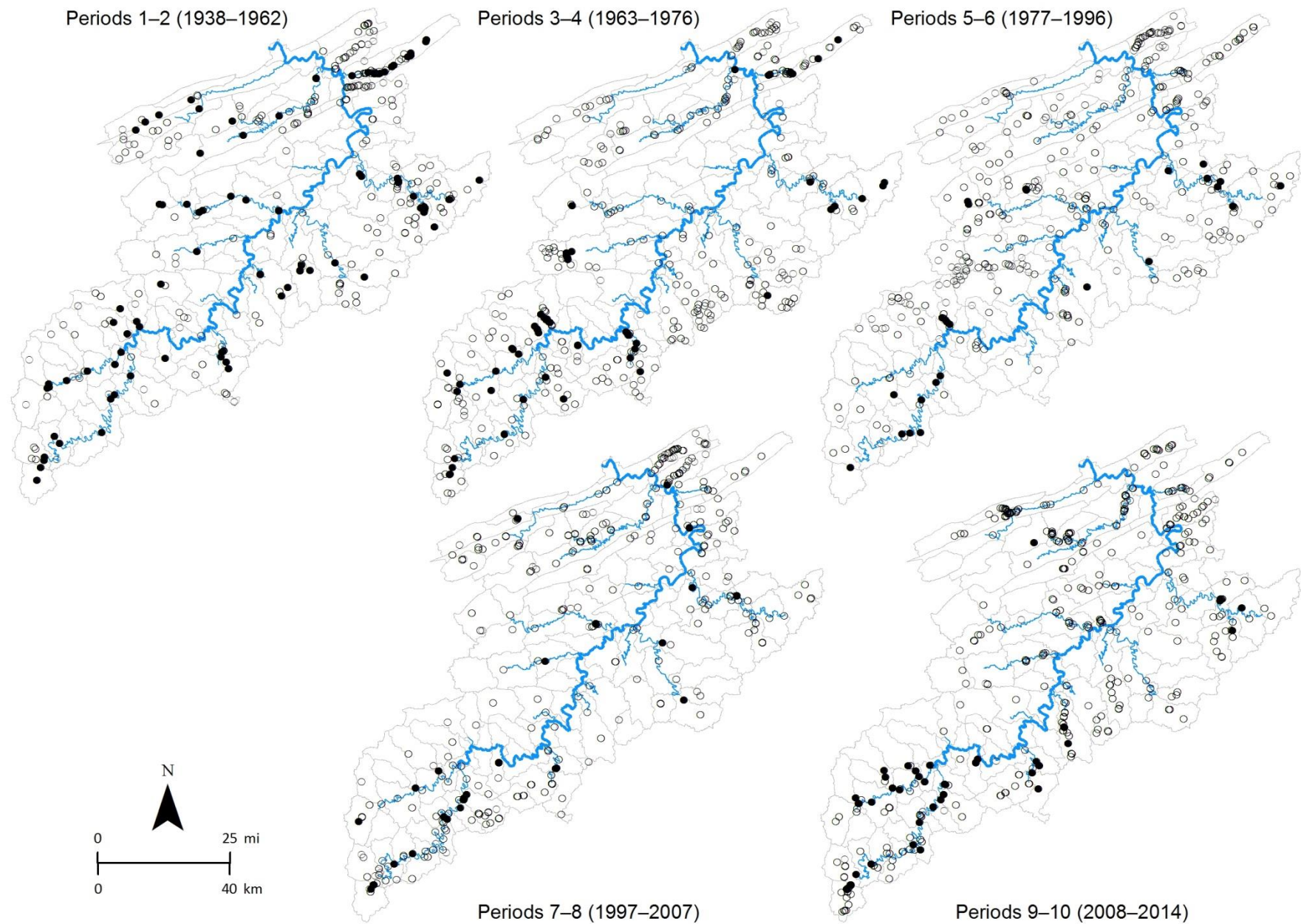
Fig. S6 Time-series maps of rosyside dace *Clinostomus funduloides* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
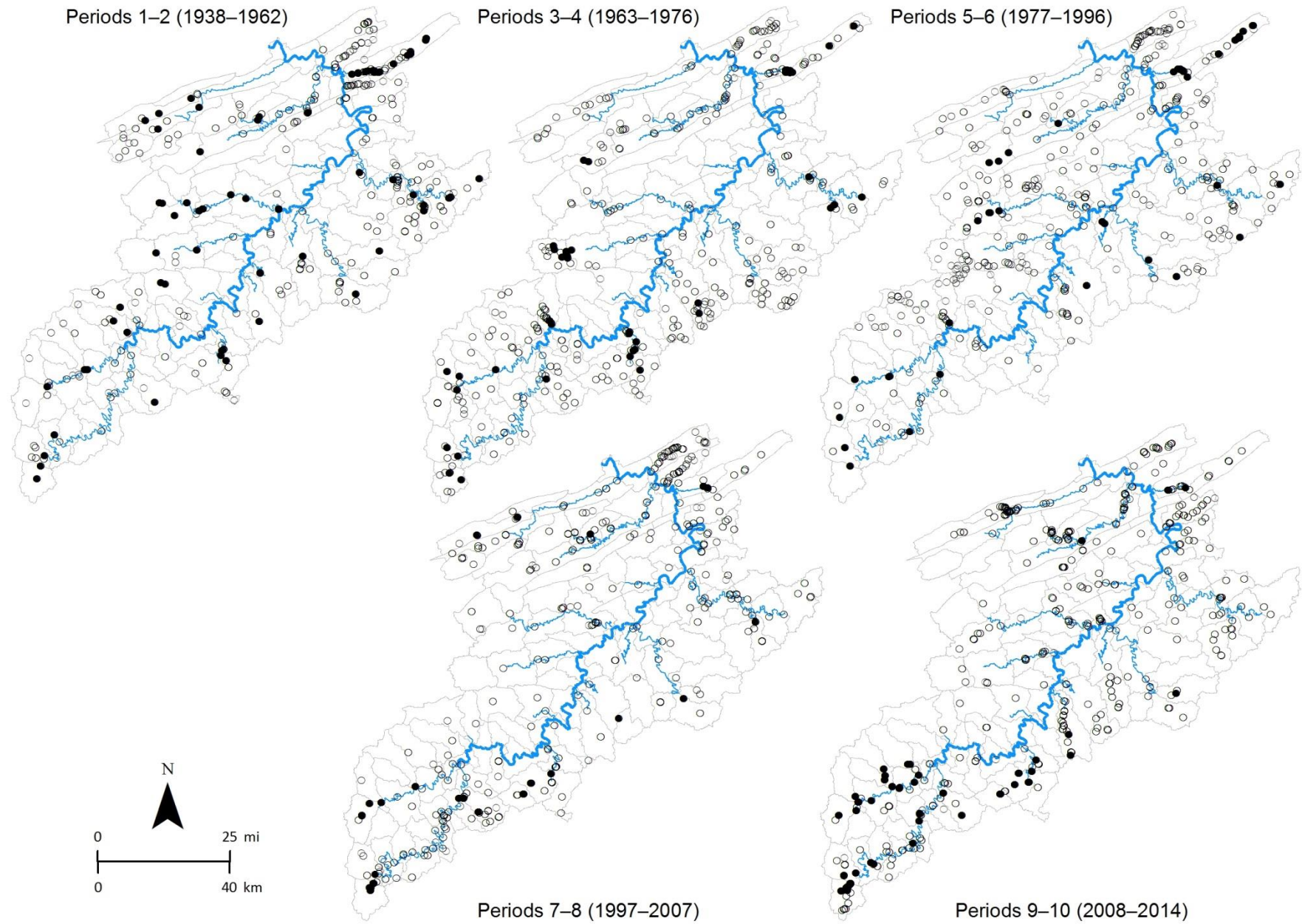
Fig. S7 Time-series maps of tonguetied minnow *Exoglossum laurae* (decliner) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
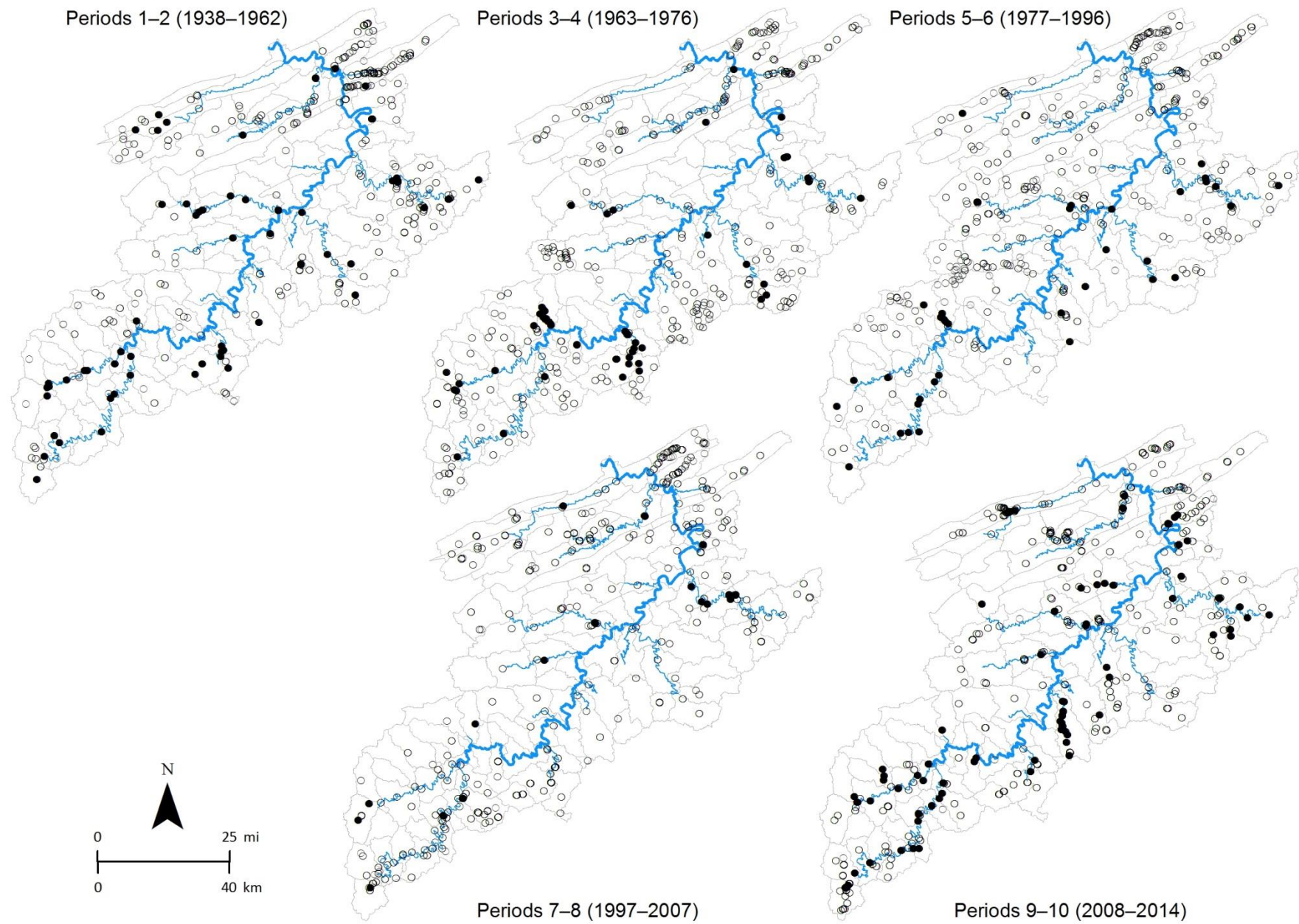
Fig. S8 Time-series maps of rosyface shiner *Notropis rubellus* (decliner) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
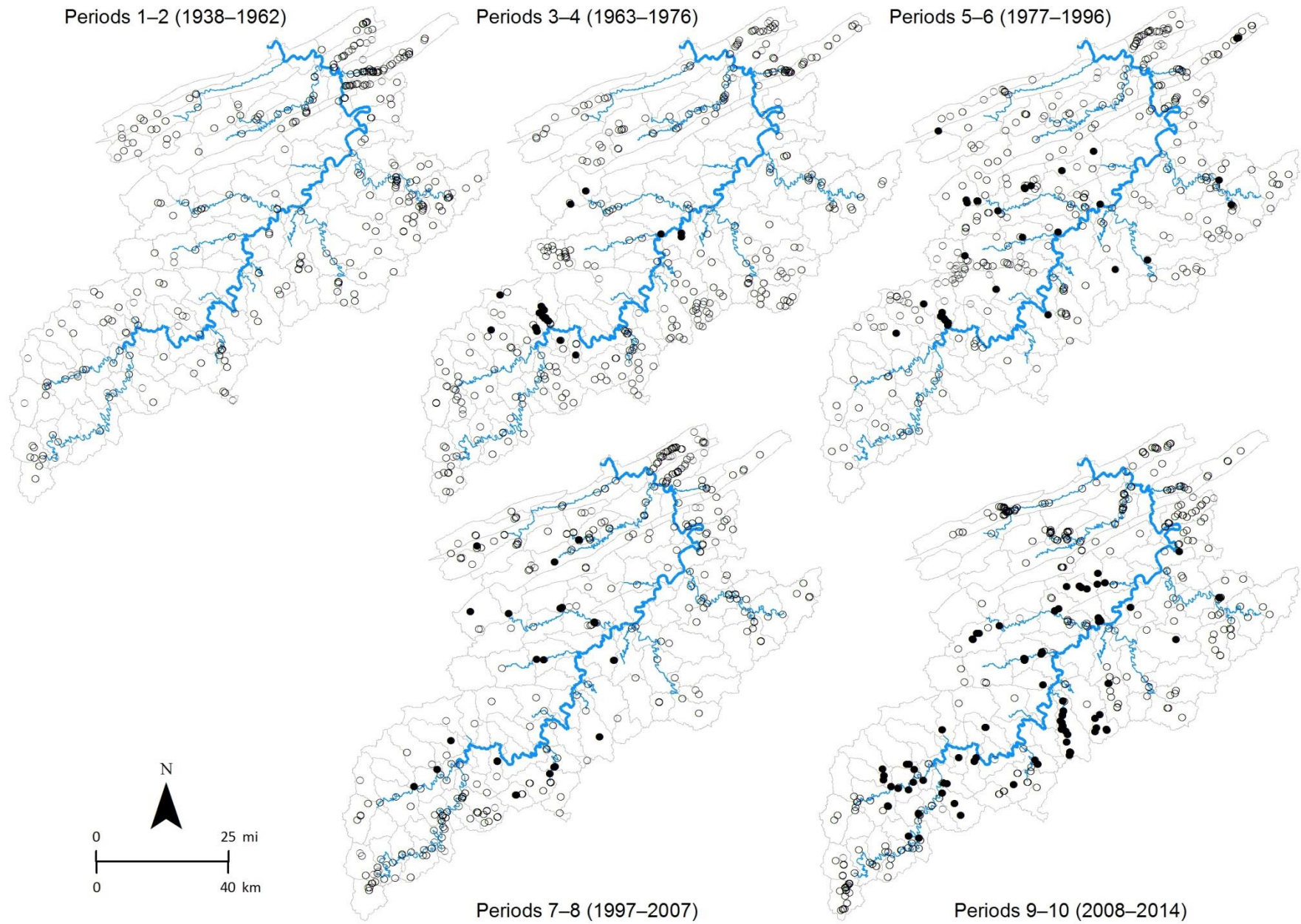
Fig. S9 Time-series maps of saffron shiner *Notropis rubricroceus* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.

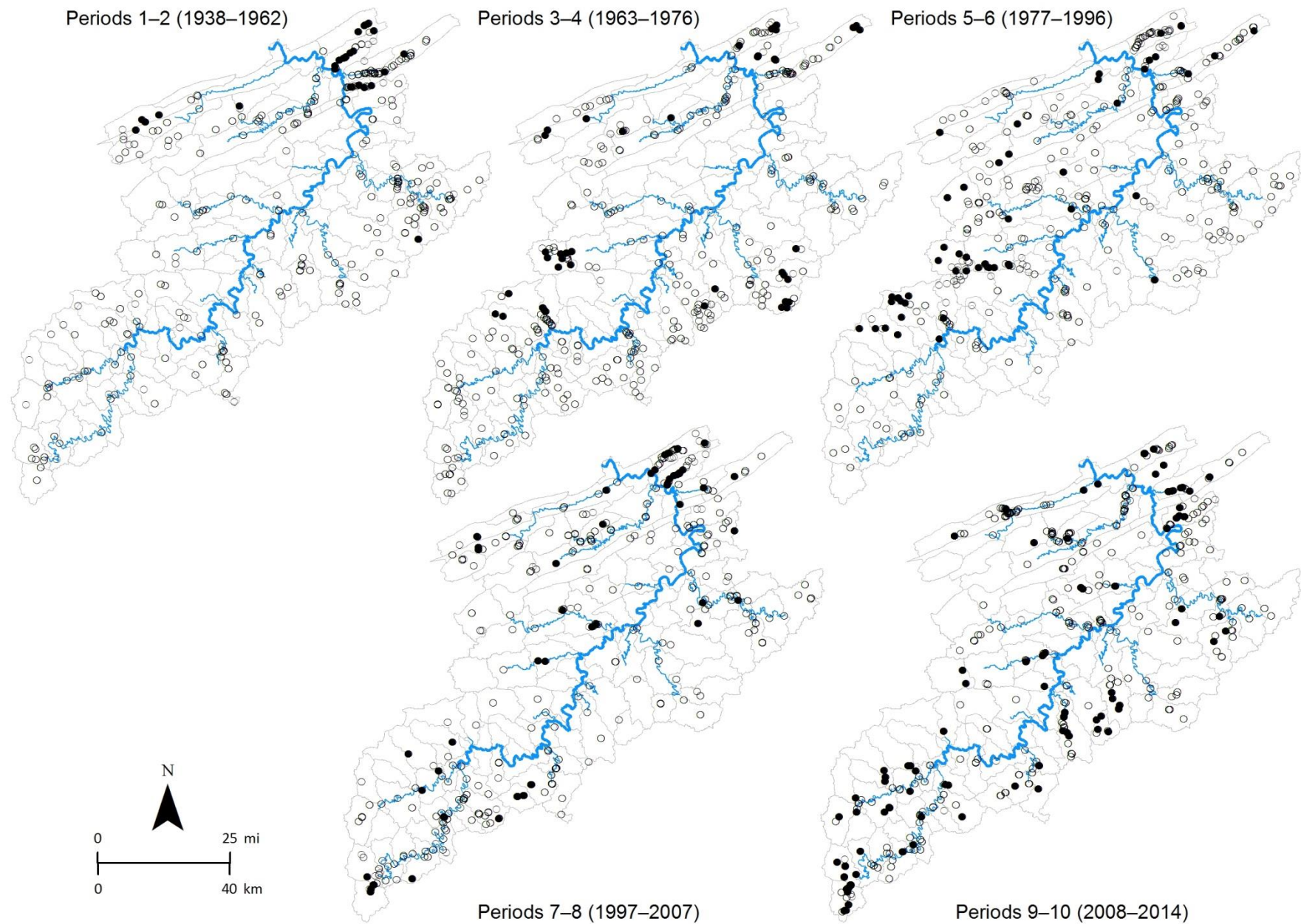**Fig. S10** Time-series maps of silver shiner *Notropis photogenis* (decliner) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
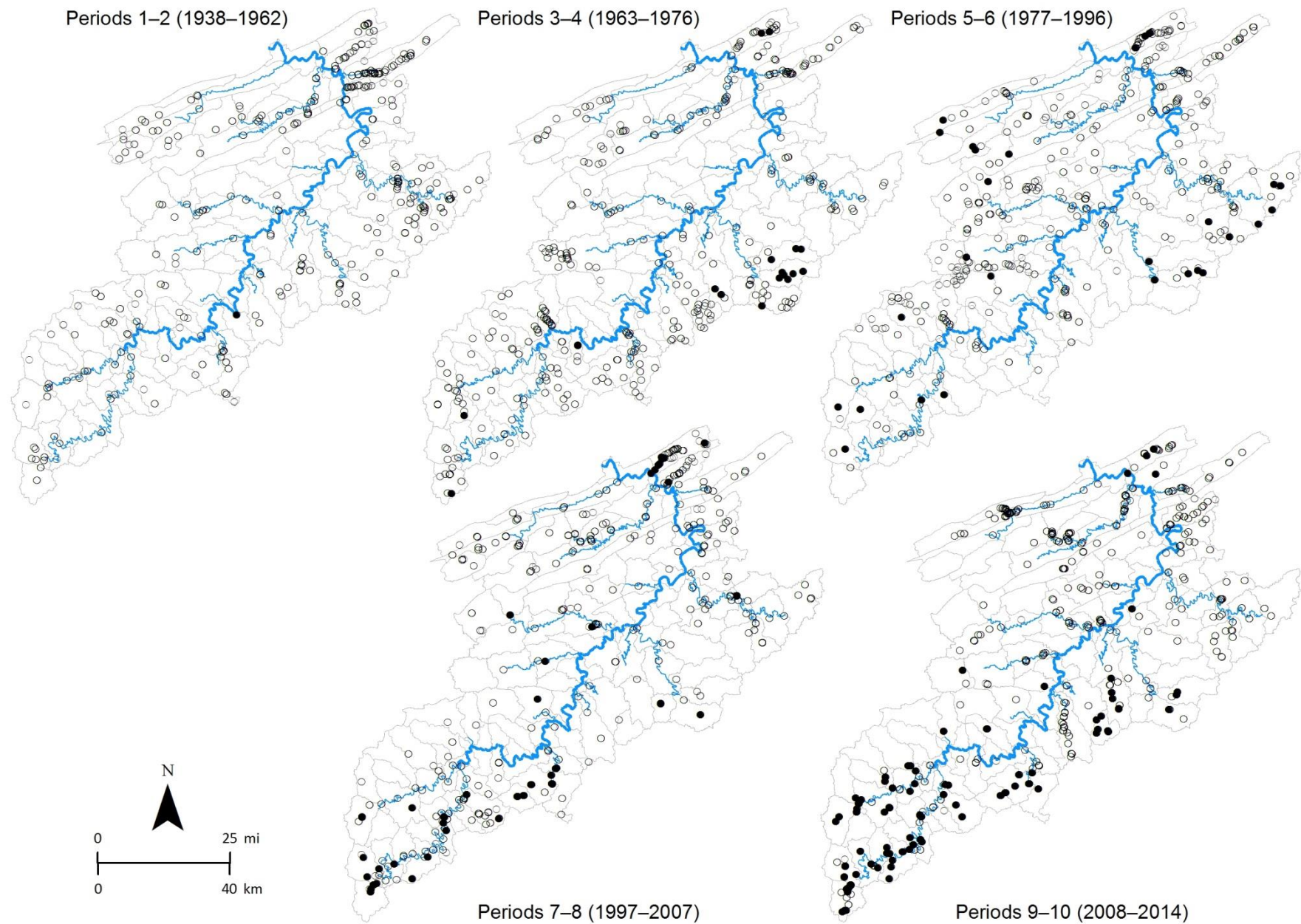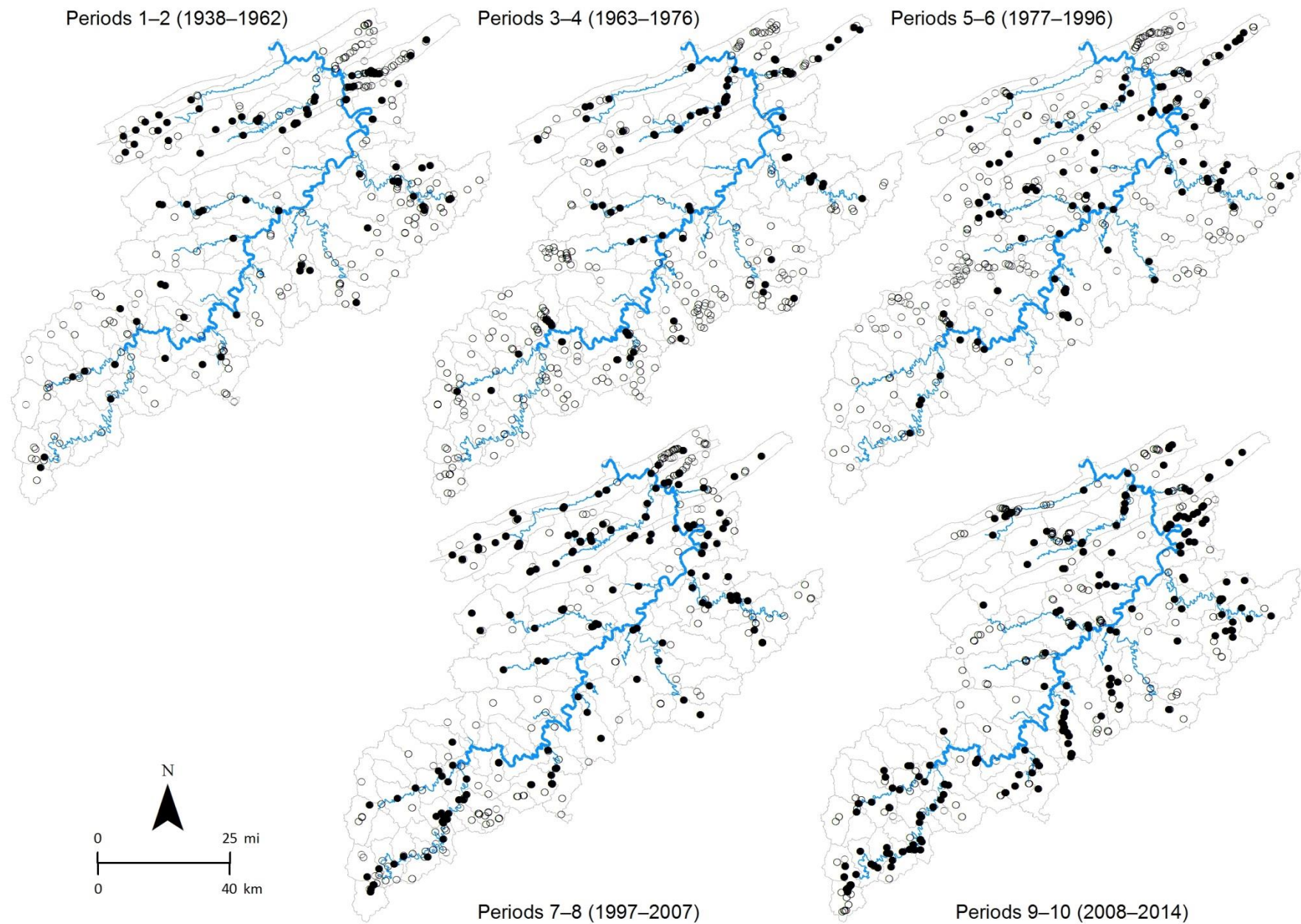
Fig. S11 Time-series maps of brown trout *Salmo trutta* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.

Fig. S12 Time-series maps of rainbow trout *Oncorhynchus mykiss* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.

Fig. S13 Time-series maps of rock bass *Ambloplites rupestris* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
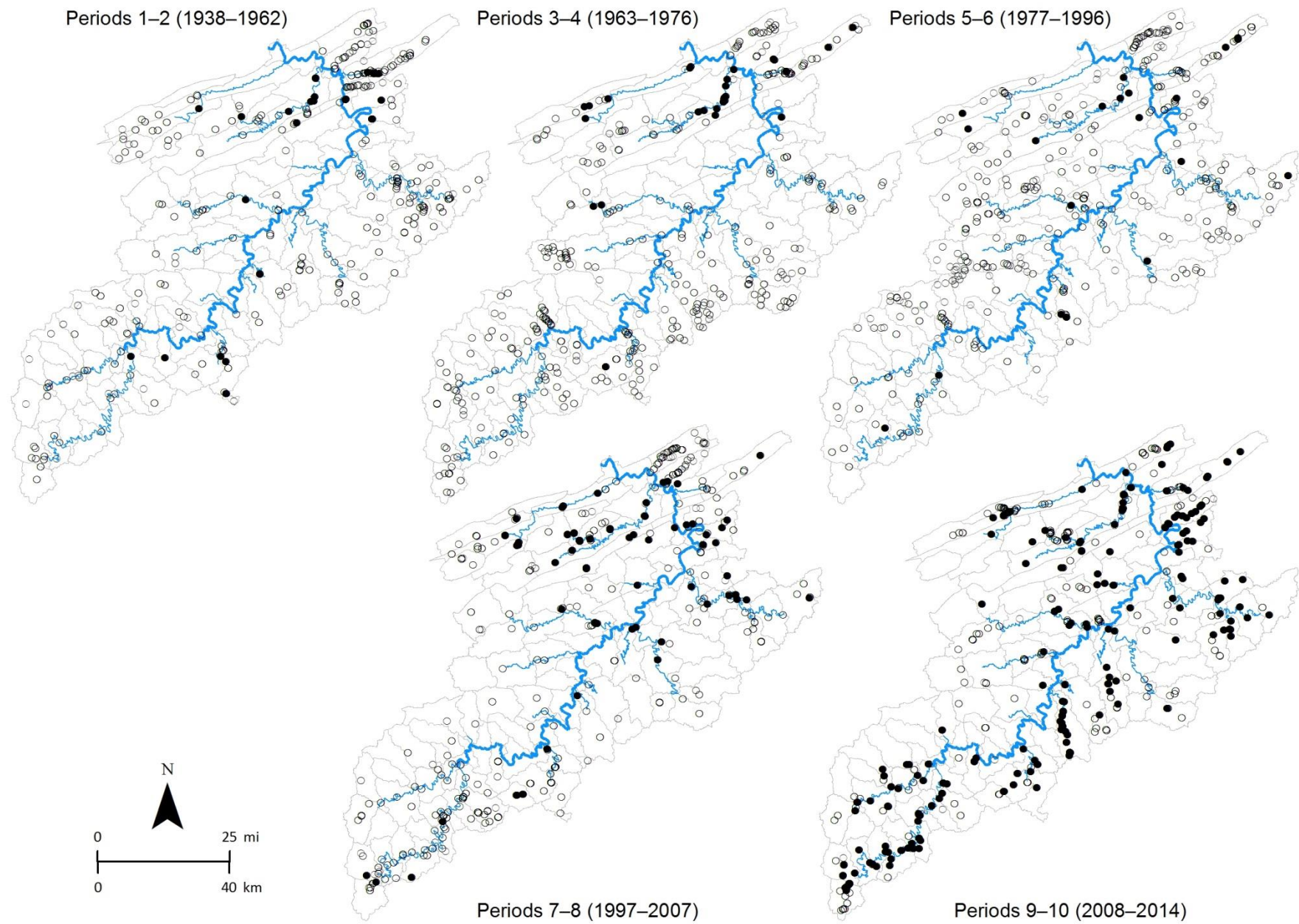
Periods 1–2 (1938–1962)

Periods 3–4 (1963–1976)

Periods 5–6 (1977–1996)

Periods 7–8 (1997–2007)

Periods 9–10 (2008–2014)

N

0 — 25 mi

0 — 40 km

128

Fig. S14 Time-series maps of redbreast sunfish *Lepomis auritus* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
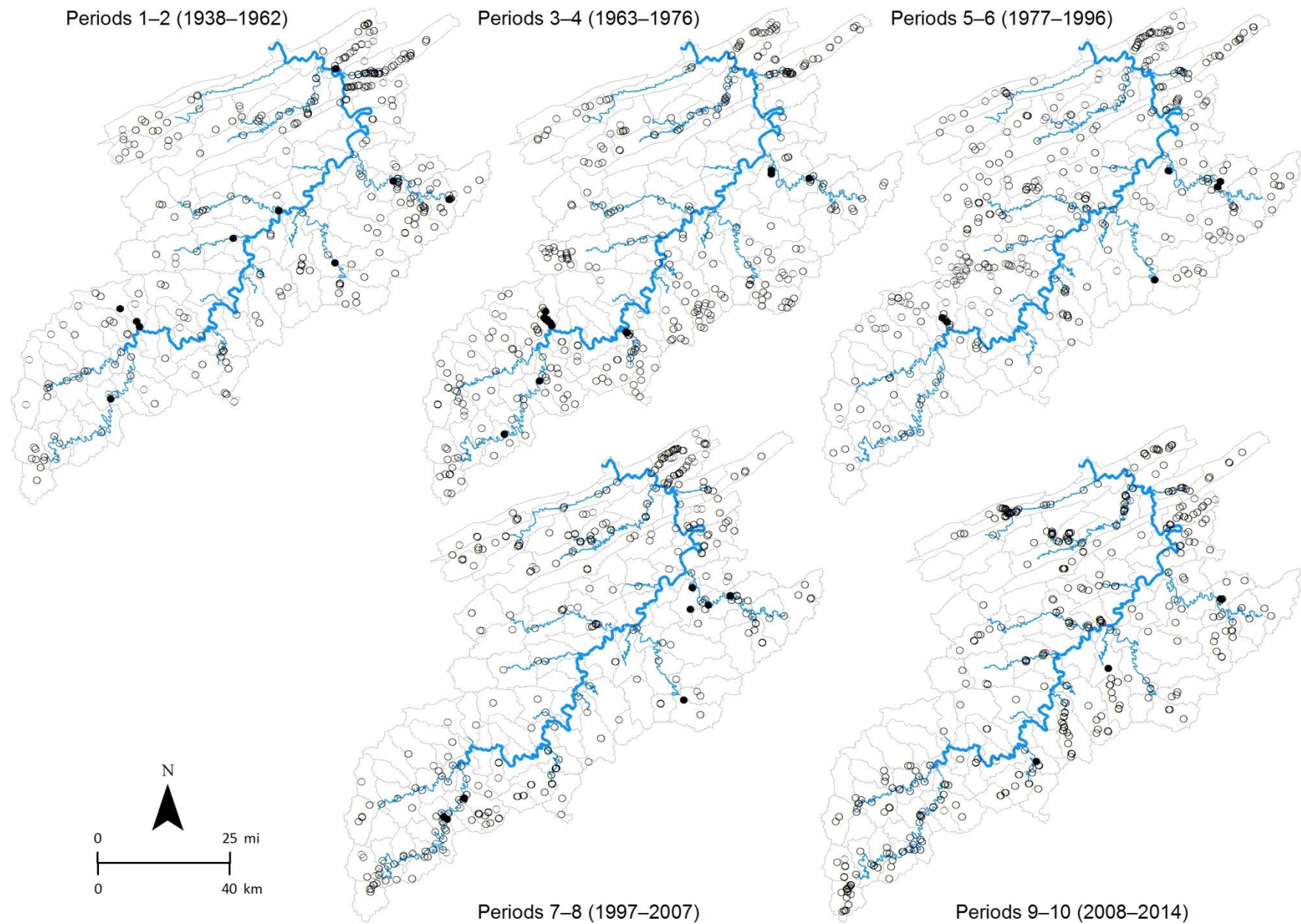
Fig. S15 Time-series maps of sharpnose darter *Percina oxyrhynchus* (decliner) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.
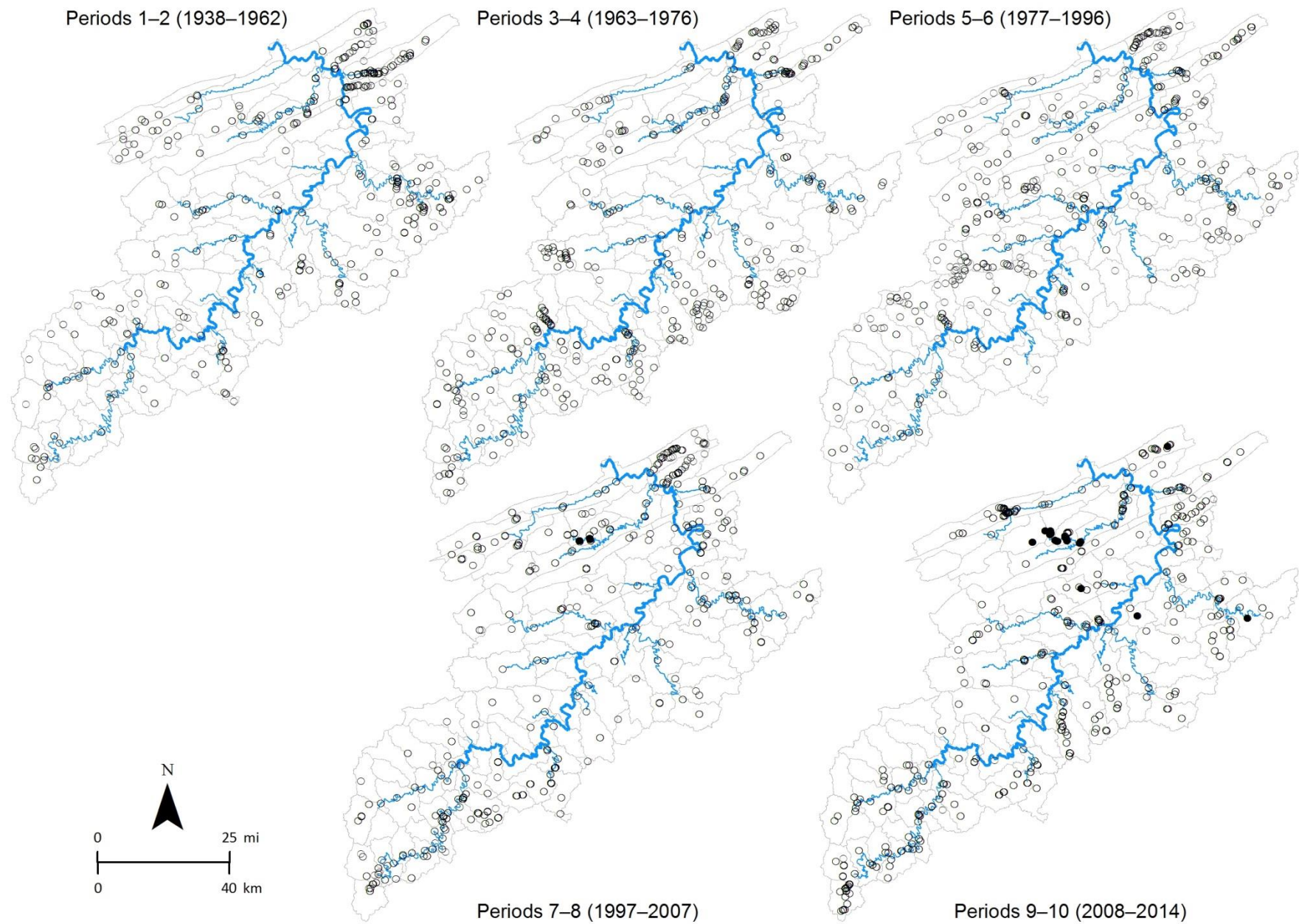
Fig. S16 Time-series maps of rainbow darter *Etheostoma caeruleum* (strong spreader) occurrence in upper and middle New River tributaries. Symbols were defined as in Fig. S4.

130