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RESEARCH ARTICLE

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Predicting the influence of river network configuration, biological traits and habitat quality interactions on riverine fish invasions

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Abstract

Aim: The relationships between species and their landscape are important for understanding migration patterns. In fluvial systems, the complexity of the river network can strongly influence the dispersal and colonization rates of invading alien fishes, but habitat quality, species' biological traits and their location of introduction are also potentially important. However, understandings of how these factors interact in the wild to influence the spatial distribution of invasive species over time are limited from empirical studies.

Location: "Virtual" and "real-world" rivers from England and Wales.

Method: We developed an individual-based model (IBM) to predict how these different factors influenced the invasion dynamics and population growth rates (as abundances) of nine "virtual" alien fishes over two timeframes (10 and 30 years). The alien fishes differed in their demographic (r- to K-selected) and dispersal (fast to slow) characteristics and the rivers in their network complexity.

Results: Irrespective of river type, species and timeframe, the main drivers of both dispersal and population growth were the location of the introduction and the mean habitat quality of the patch into which the species were released. The introduction location determined whether dispersal was mainly passive in a downstream direction (faster) or active in an upstream direction (slower), with higher habitat quality then enabling faster population growth rates. Over 30 years, invasion rates were predicted to increase as the complexity of the river network increased, as this opened multiple invasion fronts where the invader traits favoured faster dispersal.

Main conclusions: This novel IBM revealed how the complexity of the physical environment interacts with the biological traits of alien species to influence invasion outcomes, with the location of the introduction and its habitat quality being the most important factors. These results thus substantially increase understanding of the factors that influence the dispersal and colonization rates of alien freshwater fishes.

1 | INTRODUCTION

The relationships between animal movements and the structure of their environment are important to understand, with the variability in these movements driven both by species' ecology and the spatio-temporal scale being considered (Roberts & Angermeier, 2007). Relationships between animal movements and their environment are especially important in the context of newly introduced alien species, as they will determine the species' rate of spread, and hence potential negative ecological impacts (Davis & Darling, 2017; Fraser et al., 2015; Ross et al., 2001). In alien plants, simulated invasion dynamics have revealed the importance of both the connectivity of the entire landscape and the structure of the local landscape (e.g. the presence of corridors), as well as the species' dispersal ability (Andrew & Ustin, 2010). Assessments of how newly introduced alien species invade novel landscapes thus requires understanding of how the landscape structure impacts upon the main processes that contribute to their spread (Grant et al., 2007; Lurgi et al., 2016), especially dispersal (important for successful colonization) and demography (important for successful population establishment) (With, 2004).

The range expansion/spread of alien species requires their ability to move from colonized into novel areas (Havel et al., 2015). For some freshwater alien taxa, adaptations for persisting in temporary environments can assist their overland dispersal by passive or active means (Havel et al., 2015), such as the cryptobiosis of rotifers (Wallace & Snell, 2001). For alien fishes, however, their natural dispersal from invaded to uninvaded areas requires some level of fluvial connectivity (Gozlan et al., 2010), and while canals can provide movement corridors between river catchments (Hickley, 1986), movements and dispersal rates within catchments are dependent upon the structure and connectivity of the river network (Goldberg et al., 2010). This structure and connectivity will also affect the potential movements and distributional shifts in native species as they respond to the invasion (Crowl et al., 2008).

River networks are branched, corridor-like structures that have a number of sources (headwaters) and a mouth (where it joins either the sea or a lake); the distribution of branches (tributaries) and confluences determines the shape of the network, which can be classified using stream order methods (Shreve, 1966; Strahler, 1957). They can be considered as landscapes in which a set of patches form a dendritic structure that is arranged in a non-linear, spatially explicit manner (Goldberg et al., 2010). The directional flow of water within the network means that for two adjacent patches, one will be downstream from the other, and this will influence the movement of fish between them, such as whether the movement is more likely to be active (upstream direction) or passive (downstream direction) (Goldberg et al., 2010). These fish movements continue until a

confluence is encountered, when a decision is required as to which branch the fish enters. Branching is often asymmetric, as one channel is often larger than the other and has a different flow regime, and this can strongly influence the decision over which branch is taken (Byers & Pringle, 2006). These inter-patch movements are likely to be influenced by factors including the fish life-stage and their dispersal abilities (Goldberg et al., 2010; Phang et al., 2016). They will also depend on habitat quality of the patches, where there can be a higher energetic cost for a fish for settling into a lower versus higher habitat quality patch due to, for example reduced prey availability, that increases their searching time (Phang et al., 2016).

Understanding the colonization rates of alien fish in river networks is crucial for conservation management, including protecting native communities from the adverse impacts of alien invasions, especially as the ability to manage invasive fishes in the environment is inversely proportional to the extent of their spatial spread (Britton et al., 2011; Rytwinski et al., 2019). For an invasive freshwater fish whose distribution is still spatially limited within rivers, eradication can be a feasible option for eliminating their impacts on native species, whereas for those invaders that are spreading rapidly, control and/or containment methods are usually the only feasible options (Britton et al., 2011). The traits of invasive fish also often differ between the "invasion front" and the areas where the population has already colonized ("invasive core"): individuals at the front are more likely to express "dispersal-enhancing traits" that provide them with the highest probability of dispersal success (Masson et al., 2018). There are, however, considerable knowledge gaps on how the interactions of the spatial variability in river network complexity and habitat quality with the location of the release site influence the invasion success of alien fishes, especially across species of differing dispersal abilities and life-history traits. While this is likely to relate to the complexity of these interactions and a lack of empirical data (Dominguez Almela et al., 2020), recent increases in computing power and the development of individual-based models (IBM) enable the use of predictive approaches to help overcome these knowledge gaps (Day et al., 2018; Rodríguez-Rey et al., 2019).

The aim of this study was thus to determine how the invasion of alien river fishes is likely to be influenced by river network complexity and habitat quality, the location of their introduction into the network and how this varies across a range of species' dispersal abilities and life-history traits. An IBM was developed and parameterized to predict how these factors interacted to influence the rates of population increase and range occupancy of nine example alien fishes over time scales of 10 and 30 years in a range of virtual and real-world river networks. We posit that (a) river network complexity and spatial differences in habitat quality are a major determinant of the colonization rate of alien fishes, such that more branched networks

are colonized faster than less branched networks through the formation of multiple invasion fronts; (b) the introduction location in the network influences the colonization rate, such that introductions in upstream locations result in more rapid colonization and population growth due to fish movements in a downstream direction into areas of higher stream order (and habitat quality); and (c) alien fishes with higher dispersal abilities and life-history traits that facilitate fast establishment (i.e. *r*-selected traits; Dominguez Almela et al., 2020) will colonize river networks more rapidly than fishes with the opposite suite of traits.

2 | METHODS

2.1 | River networks

Two sets of river networks were used: (a) randomly generated, virtual river networks that enabled predictions to be made on channel configurations whose physical differences were constrained with a set of rules: total size of catchment, number of cells and number of confluences (maximum stream order of 4); and (b) actual river networks that enabled testing of the predictions from (a) using "real-world" configurations with natural network variability between them.

2.1.1 | Randomly generated virtual river networks

Virtual river channel networks were built using the "*OCNet*" package in "R version 4.0.1" (Carraro et al., 2020; R Core Team, 2020). The configuration of the initial state of the network had four possible values (Factor Shape, "S"): "I" (representing a valley); "T" (T-shaped drainage pattern); "V" (V-shaped drainage pattern); and "H" (hip roof drainage pattern). Three catchments per configuration type were created (Factor Catchment, ID; Figure 1), and all 12 rivers had a similar number of confluences in their network (mean = 48.6 ± 0.76 (*SD*)). The network distance from the outflow point was used to develop raster maps of habitat quality (as described below) of cell size 50 m using "ArcGIS Pro," where catchments were divided into sections limited by the river nodes. The network distance from the mid-point of each section to the outflow point was converted to a quality score by:

$$\text{Quality}_{\text{virtual rivers}} \, (\%) = 100 - \frac{\text{Distance} \times 100}{max \, (\text{Distance})}$$

Using this formula, habitat quality for the alien fish increased with distance downstream, and so habitat quality increased as stream order increased (Matthews, 1986; Smith & Kraft, 2005). The rationale behind this assumption was that as river width increased with distance downstream, this would increase the heterogeneity of the habitat (e.g. increased size and complexity of littoral areas) that, overall, would enhance habitat quality for fish. While this can be considered a simplification of habitat quality, it meant that a single variable that relates to stream order and is relevant to alien fishes could be used (Smith & Kraft, 2005).

2.1.2 | Real-world river networks

Seven river catchments in England and Wales, chosen in relation to their geographic spread and differences in their network configurations, were extracted from Ordnance Survey data: Frome, Stour, Rother, Great Ouse, Esk, Weaver and Conwy (Figure 2). Tiles of geometric mark-up language from OS MasterMap Water Network data (Ordnance Survey, 2021) were converted into shapefiles using "QGIS 3.16.3," and the individual rivers were cleaned, removing minor drainage branches (width ≤1 m), using "ArcGIS Pro." The mean width of the channels was used to develop raster maps of habitat quality of cell size 50 m using "ArcGIS Pro" by

$$\text{Quality}_{\text{actual rivers}} \, (\%) = \text{width} \times 2$$

$$\left\{ 100 \, \text{for Quality}_{\text{actual rivers}} > 100 \right\}$$

As with the virtual river networks, as the river width increased, so did the habitat quality for the alien fish. However, unlike the virtual river networks, mean channel widths of real rivers are inherently variable, and so although there were general patterns of wider sections increasingly occurring with distance downstream, areas of wider widths could also be found in more upstream areas.

2.2 | Modelling the invasion of alien fish species

The platform "RangeShifter 2.0" (Bocedi et al., 2014, 2020) was used to build a spatially explicit individual-based model for a virtual invasive fish species with a stage-structured life-cycle, juveniles (<1 year old), sub-adults (1–2 years) and adults (over 2 years) as per Dominguez Almela et al. (2021). The model was implemented using a cell-based approach (see Table 1 for full list of parameters). Reproduction was set to occur annually, after which all individuals could migrate up to once during their lifetime. The transfer phase of dispersal was modelled using the stochastic movement simulator (SMS; Palmer et al., 2011), for which the relative cost of movement was set inversely to a cell's habitat quality (i.e. it is more costly for an individual to move upstream and into areas of poorer habitat quality). In many fish species, there is a tendency for mature males to arrive on spawning grounds before females and leave last in order to maximize their reproductive fitness, so males could settle in any non-natal cell. Mature females could only settle in cells where males were already present.

For the virtual river networks, nine models were then constructed using a set of invasive-like species (Factor "SpID"), extracted from Dominguez Almela et al. (2021) and adapted to a
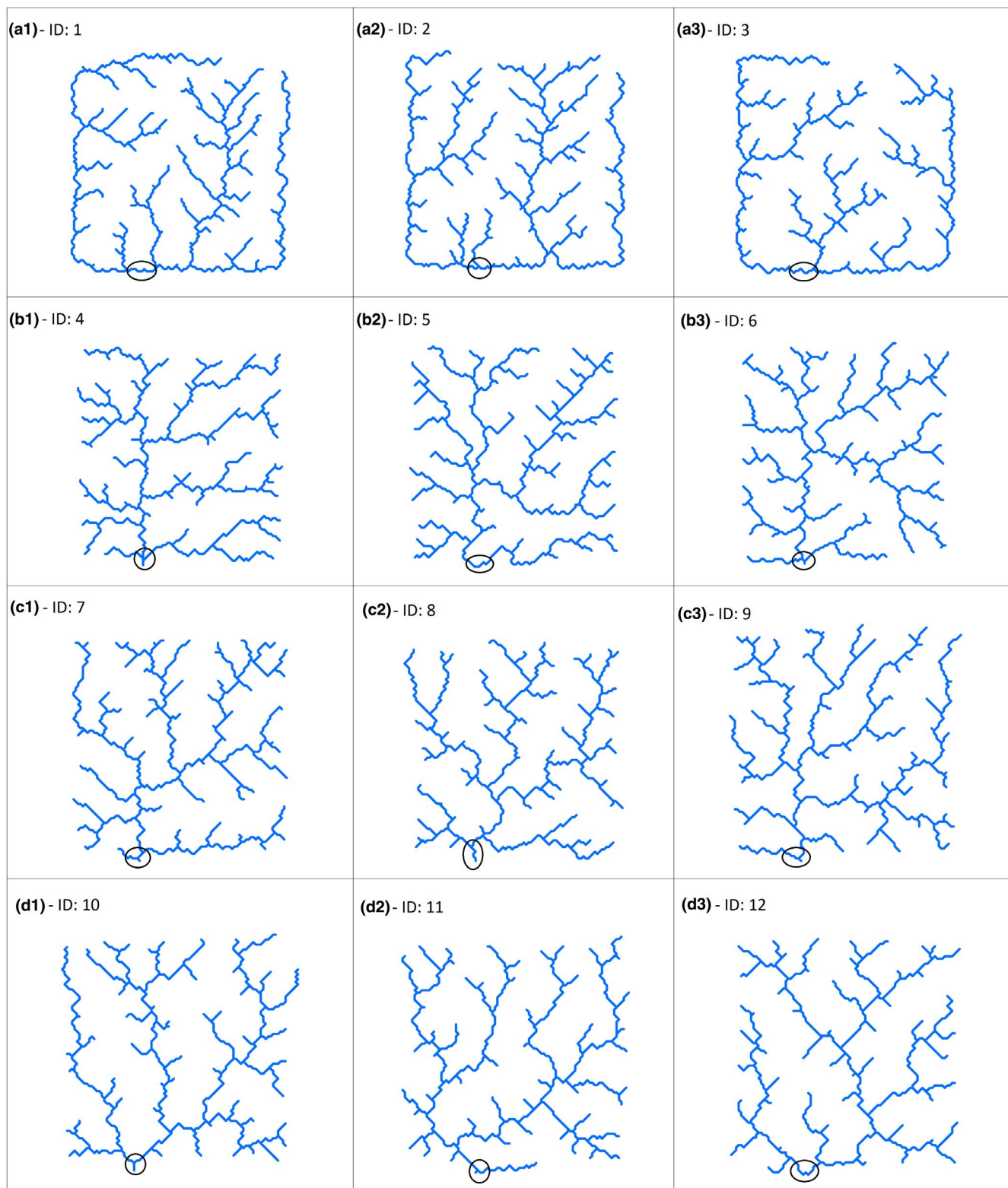
FIGURE 1 Randomly generated virtual river networks. a1-3 "H" shape; b1-3 "I" shape; c1-3 "T" shape; and d1-3 "V" shape. The outflow point is shown by a black circle

cell-based model (Table 2). These species demonstrated biological characteristics ranging from K-selected, intermediate demography to r-selected traits (Factor "SpType"), and within each group they could have either fast, intermediate or slow dispersal abilities (Factor "SpDispType"). For the real-world river networks, the same set of species were used in a cell-based model to test how the predictions from the virtual catchments represented those derived from real-world contexts.

FIGURE 2 Digitized river catchments
in England and Wales

TABLE 1 Demographic and dispersal parameters used in the IBM implemented in "RangeShifter"

	Model parameter	Stage structure	Density dependence	Value
Population dynamics	Number of reproductive seasons/year	Adults	No	1
	Proportion of males	Whole population	No	0.5
	Probability of reproducing	Adults	No	1
Emigration	Slope	Whole population	No	10
	Inflection point	Juveniles	No	0
		Sub-adults	Yes	0.48
		Adults	Yes	1.23
Transfer	Directional persistence	Whole population	No	1.5
	Perceptual range (m)	Whole population	No	50
	Memory size (cells)	Whole population	No	2
Settlement	Max. no. of steps	Whole population	No	100
	Slope	Whole population	Yes	−10
	Inflection point	Whole population	Yes	1

TABLE 2 The demographic and dispersal parameter values used in the IBM implemented in "RangeShifter"

Parameter	Strongly K-selected	Intermediate demography	Strongly r-selected
Fast disperser	**Species 1**	**Species 2**	**Species 3**
Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.4	0.4	0.4
Max. emigration probability in sub-adults	0.7	0.7	0.7
Max. emigration probability in adults	0.9	0.9	0.9
Max. settlement probability	0.013	0.013	0.013
Per-step mortality	0.0045	0.0045	0.0045
Intermediate dispersal	**Species 4**	**Species 5**	**Species 6**
Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.1	0.1	0.1
Max. emigration probability in sub-adults	0.18	0.18	0.18
Max. emigration probability in adults	0.18	0.18	0.18
Max. settlement probability	0.025	0.025	0.025
Per-step mortality	0.0045	0.0045	0.0045
Slow disperser	**Species 7**	**Species 8**	**Species 9**
Fecundity	30	63.77	180
1/b (inds/ha)	823.73	1750.96	4942.34
Survival probability in juveniles	1	0.93	0.8
Survival probability in sub-adults	1	0.89	0.2
Survival probability in adults	0.5	0.4	0.1
Max. emigration probability in juveniles	0.01	0.01	0.01
Max. emigration probability in sub-adults	0.05	0.05	0.05
Max. emigration probability in adults	0.14	0.14	0.14
Max. settlement probability	0.06	0.06	0.06
Per-step mortality	0.0045	0.0045	0.0045

For model initialization, three rules were set that marked the release point for the virtual alien fish (Factor Release point, "R"): upstream (stream order ≤2), mid-catchment (stream order: 2 to 3) and downstream (stream order: 4) (Figure 1). The initial population sizes used for each initialization rule were similar (random generated river networks: mean 3857 ± 61 (SD); real-world rivers: mean = 5575 individuals ± 80 (SD)). The initial population sizes between the simulated and real-world river systems differed due to the real-world rivers being larger and having higher quality habitats compared to the virtual rivers. Raster cost maps were developed using "ArcGIS Pro" that followed the assumptions from the habitat quality maps that habitat quality decreased, with an increased cost of dispersal, in cells that were closer to the headwater and/ or where the channel was narrower. The mean cell quality scores from the release points (R) were used to build the factor

variable "Mean habitat quality" (H). The number of confluences over specific distances (Factor "Dn"), described for a given release cell (which was located in the centre-most cell of the patch of initial distribution), was the sum of the number of confluence cells within a certain distance, for four distances: 500 m (D5), 1000 m (D10), 2500 m (D25) and 5000 m (D50). An additional three distances were added to analyse the real-world rivers due to their larger size: 10000 m (D100), 25000 m (D250) and 50,000 (D500) (Table 3a, b).

2.3 | Model predictions and statistics

For the virtual catchments for each virtual species, 36 models were run (12 landscapes ID × 3 release points R), resulting in 324 models overall with five replicates each. For the real-world rivers, 21 models

TABLE 3 (a) Inter-correlations between statistics; (b) means by release point (R); and (c) range of habitat quality (H) for each level of release point (R)

Random generated catchments (1)

(a1)

	H	D5	D10	D25	D50
H	1				
D5	-0.12	1			
D10	0.05	0.79	1		
D25	0.32	0.36	0.58	1	
D50	0.53	0.22	0.40	0.84	1

(b1)

	H	D5	D10	D25	D50
Down	97.9	1.17	3	10.6	27.1
Middle	57.9	1.67	4.33	16.2	30.7
Up	14.8	1.5	2.83	6.75	15.5

(c1)

	R		
	Down	Middle	Up
H	96.7–98.7	37.4–75.8	11.8–17.3

UK rivers (2)

(a2)

	H	D5	D10	D25	D50	D100	D250	D500
H	1							
D5	-0.05	1						
D10	0.05	0.71	1					
D25	-0.18	0.47	0.51	1				
D50	-0.26	0.40	0.41	0.88	1			
D100	-0.32	-0.04	0.11	0.58	0.79	1		
D250	-0.24	-0.15	0.16	0.30	0.53	0.82	1	
D500	0.04	-0.07	0.11	0.28	0.44	0.59	0.75	1

(b2)

	H	D5	D10	D25	D50	D100	D250	D500
Down	50.2	0.71	1.29	2.86	4.71	9.71	28.2	48.6
Middle	20.2	0.86	1.43	3.14	5.71	13.0	40.9	52.4
Up	8.20	0.71	1.14	3.86	6.29	11.3	28.7	45.2

(c2)

	R		
	Down	Middle	Up
H	22.8–100	12.4–31.9	7–9.4

were run for each virtual species (7 ID × 3 R) with five replicates each. Subsequent testing focused on high-level summary statistics for each replicate that compared values between the catchments and according to their major differences. Four population-level variables were extracted from the model outputs: (a) rate of population increase across 10 years (P_{10}) and (b) across 30 years (P_{30}), where 30 years was the maximum simulation period; (c) rate of change in patch occupancy across 10 years (Q_{10}); and (d) across 30 years (Q_{30}). Thus, P_{10} and Q_{10} reflected the short-term colonization rates, while P_{30} and Q_{30} were used for the medium-term. All values of P and Q were calculated following the methods from Dominguez Almela et al. (2021); for P_{10}:

$$P_{10} = \frac{\left(\text{pop}\left[\text{year} = 10\right] - \text{pop}\left[\text{year} = 1\right]\right)}{10}$$

where pop[year = 10] is the number of individuals at year 10, and pop[year = 1] is the number of individuals at year 1. Then, calculations for years 1–10 (P10), 6–15 (P15); 11–20 (P20), 16–25 (P25) and 21 to 30 (P30) were as per the formula above (other than substituting for the correct number of years), and the maximum mean annual increase in P was determined from:

$$P_{30} = max\ (P10, P15, P20, P25, P30)$$

The same approach was used to calculate the change in cell occupancy over a short period and the maximum decadal rate of (Q_{10} and Q_{30}, respectively):

$$Q_{10} = \frac{\left(\text{NOccupPatches}\left[\text{year} = 10\right] - \text{NOccupPatches}\left[\text{year} = 1\right]\right)}{10}$$

where Q_{10} is the rate of change in cell occupancy for the years 1 to 10 inclusive, NOccupPatches[year = 10] is the number of occupied cells at year 10, and NOccupPatches[year = 1] is the number of occupied cells at year 1, etc. P_{10}, P_{30}, Q_{10} and Q_{30} were then used as the response variables within linear mixed effects models (LMMs) to account for their differences across the virtual (n = 1620) and real-world rivers (n = 945). The LMMs were fitted in the R package "lme4" (Bates et al., 2015) and used to select the best-fitting model according to Akaike's information criterion (AIC). The response variables P_{10}, P_{30}, Q_{10} and Q_{30} were transformed as $y' = \log(y + c)$, where c was a constant sufficiently large to offset any negative values, and the factors species ID (SpID) and catchment ID were treated as random effects in all models. In the model fitting process for the virtual catchments, selection commenced by fitting single terms to a model for all nine species: shape (S), release point (R), habitat quality (H), number of confluences over a distance (D5–D50), species demography types (SpType) and species dispersal types (SpDispType). After retaining the best single term on the basis of the lowest AIC, additional catchment factors and their interactions were added iteratively, and the best-fitting model retained at each iteration. Finally, species effects (SpType and SpDispType) were added into the models. For the real-world rivers, a similar model

selection process involved assessment of the following factors: release point (R), habitat quality (H) and number of confluences over a distance (D5–D500). The factor catchment ID was included as a random effect, and log transformation was applied as above.

As the release points (R) and mean habitat quality (H) were always highly correlated (i.e. R for upstream reaches always had low H scores and vice versa; Table 3c), all final models were manually modified to examine the variance attributable to explanatory variables present by changing their order. The number of confluences over a distance (D5–D500) were also correlated, and only one of them was retained in the final LMMs based on the lowest AIC. The estimates of the best-fitting models were used to make predictions of P_{10}, P_{30}, Q_{10} and Q_{30} as functions of H and R (Table 3c).

3 | RESULTS

3.1 | Virtual river networks

In the virtual rivers, increased values of P_{10} and P_{30} were mainly driven by both the release point of the species (R) and mean habitat quality (H), which were highly correlated (i.e. depending which term is included first, this term explains most of the variance). In the best fitting models, R and H together accounted for 96% of the model variance in 10 years and 91% in 30 years (Table 4). Shape (S) always accounted for low variance in these models and the number of confluences (Dn) was not included in the best-fitting models for P_{10} or P_{30} (Table 4). For Q_{10}, R and H were also the most important variables (90% of variation; Table 4), but for Q_{30}, the number of confluences within 5000 m (D50) explained 91% of the variance (Table 4), the rate of range expansion increasing as the number of confluences encountered by the invader increased. P_{10} and Q_{10} were predicted to vary with H and R (Figure 3), where population growth rates would increase as the mean quality of the invaded area increased; in contrast, range expansion rates decreased as quality decreased. P_{10} and Q_{10} were predicted to be higher when the species had faster dispersal ability (Figure 3).

When considering the virtual fish species separately, the variance in P_{10} and Q_{10} was, for most species, mainly explained by R and H (P_{10}: 85–99% variance explained; Q_{10}: 85–99%; Table S1). For P_{10}, the only exceptions were the intermediate and r-selected individuals with fast dispersal, for which R and H accounted for only 5–10% of the variance (Table S1). For Q_{10}, the exceptions were fast dispersers of all three demographic types, where R and H only explained 2–4% of variance (Table S2). The influence of R and H on P_{10} and Q_{10} was lowest for fast dispersers and highest for slow dispersers; the rate of colonization and population growth for species with faster dispersal was affected more by the number of confluences (Dn), whereas species with slower dispersal rates were affected more by habitat quality (Tables S1 and S2).

For P_{30} and Q_{30}, the number of confluences (Dn) explained most of the variance in the best-fitting models across most species (P_{30}:

TABLE 4 Principal sources of variance explained (%) in the best-fitting models for rate of population increase (P_{10} and P_{30}) and rate of change of cell occupancy (Q_{10} and Q_{30}) in randomly generated catchments

| P_{10}					Q_{10}			
10 years	**Log(P + 100)**				**10 years**	**Log(Q + 10)**		
Factor	**df**	**Sum Sq**	**% variance**		**Factor**	**df**	**Sum Sq**	**% variance**
Shape (S)	3	1.5	0.3		Shape (S)	3	0.3	0.3
Release point (R)	2	447.4	93.4		Release point (R)	2	74.4	88.9
Hab. quality (H)	1	15.7	3.3		Hab. quality (H)	1	1.4	1.7
					D5	1	0.1	0.1
SpType	2	0.3	0.1					
SpDispType	2	3.5	0.7		SpDispType	2	0.6	0.8
S*R	6	10.7	2.2		S*R	6	5.9	7.1
					S*H	3	0.8	1.0
P_{30}					**Q_{30}**			
30 years	**Log(P + 10)**				**30 years**	**Log(Q + 10)**		
Factor	**df**	**Sum Sq**	**% variance**		**Factor**	**df**	**Sum Sq**	**% variance**
Shape (S)	3	1.2	0.7		Shape (S)	3	0.2	1.0
Release point (R)	2	132.9	88.6		Release point (R)	2	0.0	0.0
Hab. quality (H)	1	3.4	2.3		Hab. quality (H)	1	0.0	0.0
					D50	1	17.8	90.8
SpType	2	2.7	1.8					
SpDispType	2	0.2	0.1		SpDispType	2	0.2	1.2
S*R	6	9.8	6.5		S*R	6	1.4	7.0
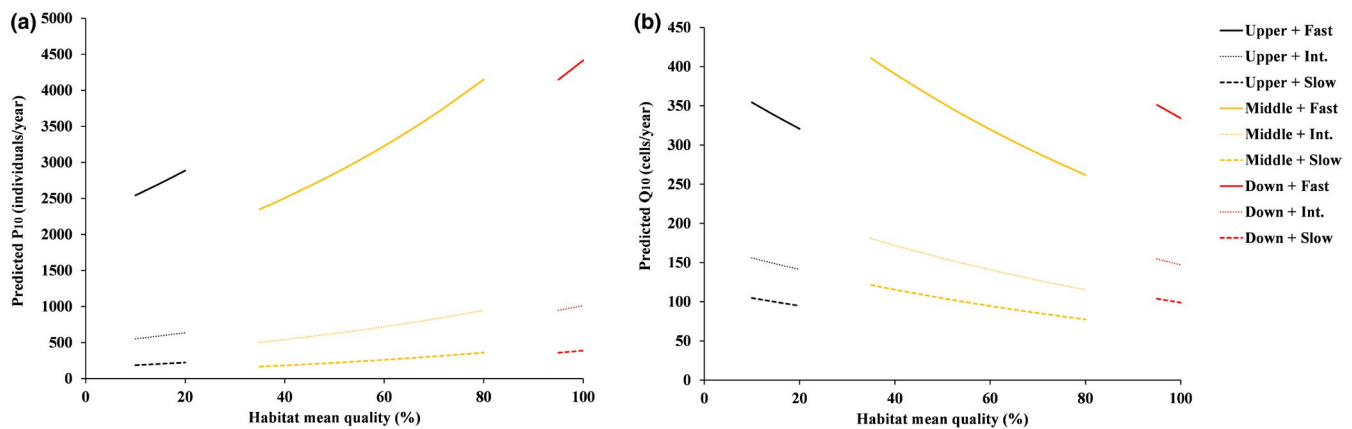
FIGURE 3 (a) Predicted rate of population growth (P_{10}) for each release point (R) vs. release point mean habitat quality (H) in virtual catchments. (b) Predicted rate of change in cell occupancy (Q_{10}) for each release point (R) vs. release point mean habitat quality (H) in virtual catchments. V-shaped drainage pattern and Dn = 5 applied

55–75% variance explained; Q_{30}: 50–93%; Tables S1 and S2). For P_{30}, the exceptions were one intermediate and two slow dispersers (0.04–0.4% variance explained) (Table S1); for these species, R explained most variance, which, together with H, explained 86–99% (Table S1). For Q_{30}, the exceptions were two slow dispersers, where again R was the best explanatory variable (82–94% of variance) (Table S2).

3.2 | Real-world river catchments

Model predictions of the rate of population growth (P_{10} and P_{30}) of the nine virtual alien species revealed that the best-fitted models included H and R, which together explained 97% of the variance in 10 years and 93% in 30 years, leaving only a small percentage explained by Dn (P_{10}: 2%; P_{30}: 5%; Table 5). As H increased, the

DOMINGUEZ ALMELA ET AL.

TABLE 5 Principal sources of variance explained (%) in the best-fitting models for rate of population increase (P_{10} and P_{30}) and rate of change of cell occupancy (Q_{10} and Q_{30}) in real-world rivers

| P_{10}				Q_{10}			
10 years	**Log(P + 170)**			**10 years**	**Log(Q + 20)**		
Factor	**df**	**Sum Sq**	**% variance**	**Factor**	**df**	**Sum Sq**	**% variance**
Hab. quality (H)	1	333.1	62.0	Hab. quality (H)	1	32.8	41.0
Release point (R)	2	189.0	35.2	Release point (R)	2	44.0	55.1
D5	1	10.9	2.0	D25	1	1.2	1.6
SpDispType	2	3.8	0.7	SpDispType	2	1.3	1.6
H*R	2	0.9	0.2	H*R	2	0.6	0.7
P_{30}				Q_{30}			
30 years	**Log(P + 140)**			**30 years**	**Log(Q + 20)**		
Factor	**df**	**Sum Sq**	**% variance**	**Factor**	**df**	**Sum Sq**	**% variance**
Hab. quality (H)	1	184.7	63.1	Hab. quality (H)	1	4.6	28.7
Release point (R)	2	88.1	30.1	Release point (R)	2	7.9	49.7
D5	1	14.9	5.1	D10	1	1.5	9.7
SpDispType	2	3.0	1.0	SpDispType	2	1.4	8.9
H*R	2	1.7	0.6	H*R	2	0.5	3.0
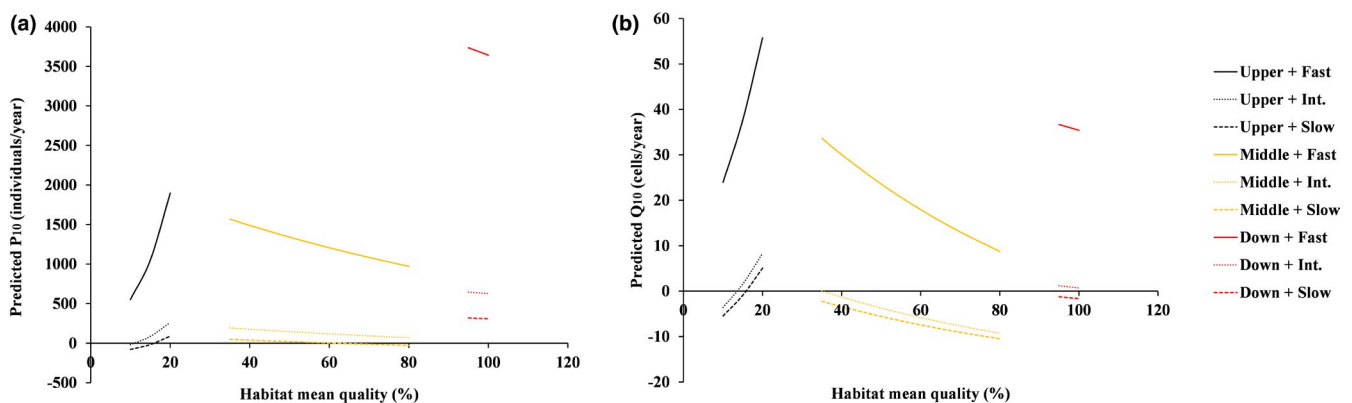
FIGURE 4 (a) Predicted rate of population growth (P_{10}) and (b) predicted rate of change in cell occupancy (Q_{10}) for each species dispersal type (fast, intermediate, slow) vs. release point mean habitat quality (H) in real-world catchments

population growth rate increased only for upstream releases; when the initial invaded area was either in the mid-catchment or downstream, population growth was inversely related to H (Figure 4).

For predictions of Q_{10} and Q_{30}, most model variance was again explained by H and R (Q_{10}: 96% and Q_{30}: 78%; Table 5). Approximately 10% of the variance in Q_{30} was explained by Dn within 1000 m distance and 9% was explained by the dispersal behaviour of the invader (Table 5). For upstream releases, higher rates of colonization were predicted when the initial invaded area was of higher habitat quality (Figure 4). Initial invaded areas in mid-catchment or downstream areas had an inverse relationship with H. For species of higher dispersal ability, higher rates of colonization were predicted compared to intermediate or slow dispersers (Figure 4).

At the species level, the number of confluences (Dn) was always included in the best-fitting models predicting P_{10} and P_{30}, but with the effective distance (D5 to D500) varying between species, although R and/or H were the most important explanatory variables (P_{10}: 92–99% variance explained; P_{30}: 81–99%; Table S3). For Q_{10} and Q_{30}, R and H were the most important variables in models (Q_{10}: 62–99% variance explained; Q_{30}: 51–94%; Table S4), although Dn was also highlighted in 5 out of the 9 models for Q_{30} (13–25%; Table S4).

4 | DISCUSSION

The management of alien species in the environment generally aims to minimize their impacts on the native communities and requires assessment of the current spatial distribution of the invader and predictions of how this will change over time (Britton, Gozlan,

et al., 2011). For alien riverine fishes, these assessments require information on how their dispersal rates and population demographics influence their colonization rates following their introduction (Dominguez Almela et al., 2020). Here, we applied an IBM to predict how different river network configurations and habitat quality influenced the invasion of nine virtual alien fish that varied in their dispersal abilities and life-history traits, and by the location of their introduction into the network. In both the virtual and real-world river networks, the general prediction was that both population growth and cell occupancy rates were mainly driven by the location of the introduction of the species and its mean habitat quality, as predicted, but with the configuration of the network often having a relatively minor influence, contrary to prediction. The influence of the location of introduction into the network was important as it determined the overall direction of spread, that is whether the wider range expansion of the species required upstream or downstream movements, where downstream movements had a higher benefit as they involved movements into cells of higher habitat quality. In addition, downstream movements in fish can be passive as well as active, whereas upstream movements can only be active (Benjamin et al., 2007). It was only over the longer 30-year time period that the rate of catchment colonization increased as the spreading population encountered more confluences (i.e. tributaries). This aspect was consistent with our prediction and conforms with empirical studies that suggest that invasion dynamics can be strongly dependent on changes in stream order, with larger, mainstem rivers having faster colonization rates than headwaters (Radinger & Wolter, 2014).

Network complexity was predicted to be important in the invasion success of virtual species with high dispersal ability, as increased numbers of river confluences elevated their colonization rates. The movements of the fish into numerous branches opens up a larger number of range fronts, and so the expression of high dispersal ability at numerous range fronts increases their colonization rate (Masson et al., 2018). In contrast, slow dispersers were more affected by the habitat quality of the cells into which they were introduced, as this affected their population growth during the early years of colonization. This habitat selection and condition-dependent movement can be seen in many fish species, for which the relationship between individual decisions of movement and larger-scale population dynamics over time and space are generally important for understanding the importance of movement for species' persistence (McMahon & Matter, 2006). The relationship between individual decisions and population dynamics is arguably even more important for alien species during their colonization period, given the relationship between their establishment within cells (metric Q) and the species' rate of population growth (metric P). For example, while dispersal enables movement into new cells, it has energetic, mortality risk and time costs that can decrease the probability of establishment in those new cells (Bonte et al., 2012). Longer distance dispersers also often arrive in poorer condition than those moving shorter distances (Lange & Marshall, 2016), and the quality of the individuals arriving in the new habitat is an important determinant of establishment success (Myles-Gonzalez et al., 2015). In the context

of alien fishes, while *r*-selected species with high dispersal abilities are predicted to have faster colonization rates, species with more *K*-selected life-history traits and lower dispersal ability can still be successful invaders if their trade-offs are favourable between dispersal, establishment and individual quality (García-Berthou, 2007).

Across all nine species, rivers and time frames, the location of the introduction into the river network was highly important in determining the rate of network colonization, affecting both the direction of the movement needed for colonization and the costs involved in relation to habitat quality. In real-world rivers, actual differences in channel morphology, gradient, thermal regime and physical habitat structure would strongly influence the ability of some alien fish species to survive and then establish. For example, in the River Great Ouse, a highly regulated, low energy lowland river, bitterling *Rhodeus sericeus* (small-bodied, short lifespan) and pikeperch *Sander lucioperca* (larger bodied, long life-span) are already invasive (Dominguez Almela et al., 2020; Nolan & Britton, 2019). As both of these fishes are typical of lowland rivers, they are less likely to withstand the conditions in the River Conwy, a river of higher energy running off an upland area of North Wales and where salmonid fishes are prevalent. However, invasive salmonids, such as pink salmon *Oncorhynchus gorbuscha*, which has recently appeared in Scottish and Irish rivers (Armstrong et al., 2018; Millane et al., 2019), could potentially prosper in the Conwy, but would be unlikely to be able to enter the Great Ouse due to flood regulation structures acting as barriers to upstream movement. These real-world considerations are important, as they highlight the alien species most likely to invade these actual catchments, where the Great Ouse appears more vulnerable to the invasion by alien fishes with a wider range of traits than the Conwy. Only after these species-specific traits are considered would the location of their release be important, but with this also likely to be influenced by the actual species concerned and their ability to adapt to the new conditions. For example, rainbow trout *Oncorhynchus mykiss* is regularly released for angling into many head-waters in Britain, albeit with low invasion success (Fausch, 2007), but their ability to survive in reaches downstream is likely to be much reduced due to their requirements for relatively cool, highly oxygenated waters.

Invasive freshwater fishes can present a variety of dispersal traits, with the interaction of these traits with the river network important in determining invasion outcomes (e.g. Almeida et al., 2014; Fukuda et al., 2013). The characteristics of the area of first introduction can be an important predictor of the success of colonization as, while rivers vary considerably in their network configurations, their upper reaches tend to be relatively narrow and less suitable for fish (Kim et al., 2021). If the invader was introduced into these areas then it is likely it would need to expend considerable amounts of energy to disperse into more suitable habitats. Our simulations predicted that upstream releases resulted in higher rates of spread, mainly due to the fish being able to quickly reach the maximum carrying capacity of the low-quality cells, so they keep moving into new cells of similar or lower costs (i.e. downstream direction). Fast dispersers were predicted to colonize the real-world rivers more rapidly than

the intermediate and slow invaders. Areas that were highly branched and of good habitat quality especially positively affected fast dispersers, as these enabled the fish to invest their energy on establishing abundant populations while occupying new cells in the river.

The IBM applied here provided a predictive approach for investigating the relationship between newly introduced alien species and their novel riverine environment. While investigating these relationships empirically is difficult, predictive models can also have limitations due to their simplification of real-world situations (With, 2002). We made several model assumptions for reasons of parsimony. For example, the habitat quality of the randomly generated rivers was created with the assumption of upstream areas being of lower habitat quality according to their narrower width (i.e. through littoral areas potentially having less vegetation for refugia, and with the main channel having a higher flow regime and lower water level capacity). Indeed, many British rivers conform to this pattern, especially for alien cyprinid fishes where areas further downstream of higher stream order are more likely to provide more suitable habitats (Kim et al., 2021). While this simplified the modelling process, we acknowledge that some alien species introduced in downstream areas would be capable of moving upstream and could even pass structures that fragment the river (Starrs et al., 2017). Our model did not consider anthropogenic barriers, so the dispersal of the species was only limited by the costs of their dispersal. Given the extensive fragmentation of rivers in Britain (Jones et al., 2019), and indeed in Europe (Belletti et al., 2020) and the world more generally (Grill et al., 2019), future work should consider incorporating barriers into network configurations, especially as these barriers can affect the behaviour of freshwater organisms (Rodeles et al., 2021; Starrs et al., 2017). However, this would require an additional algorithm relating to barrier permeability, such as the ability of fish to move upstream according to river level (Davies et al., 2021), and whether the barrier incorporated a fish by-pass structure (Pereira et al., 2017). Interactions of the invading fish with the native community were also not considered within the model, and it is acknowledged that these interactions can be an important factor in the outcome of biological invasions where, for example, the extent of native biotic resistance and resilience to the invader can determine the extent of its establishment and spread (Alofs & Jackson, 2014; Svenning et al., 2014; Thompson & Fronhofer, 2019). Nevertheless, we argue that despite not being able to include the impacts of barriers on fish movements and the extent of resistance and resilience by native communities, the simulations provided a series of novel insights on the abiotic factors that influence the invasiveness of alien riverine fish and can be used within invasion risk assessment processes to help identify the most appropriate interventions (Bampfylde et al., 2010; Britton, Copp, et al., 2011; Dominguez Almela et al., 2020).

In summary, our application of this IBM has filled a considerable knowledge gap in understanding how river network complexity, habitat quality and location of introduction influence the invasion success of alien fishes of differing life-history traits and dispersal abilities. The predictions indicated that, in general, the location of the release is fundamentally important through its influence on the direction of dispersal required for the species to locate favourable habitat conditions. River network configuration was important in the longer term, such that more complex networks enabled the opening of more invasion fronts that drove an elevated colonization rate. Species with higher dispersal abilities were able to colonize networks faster, especially when they had *r*-selected traits that facilitated establishment within cells. Correspondingly, these predictions reveal that the combination of biotic and abiotic variables can affect both dispersal and establishment processes, but that can be better understood when these processes are decoupled within predictive models.

CONFLICT OF INTEREST

None of the authors have any conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used are available in the main text and supporting information.

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BIOSKETCH

Victoria Dominguez Almela has a broad interest in freshwater ecology, with a specific interest on novel applications of GIS and models to predicting ecological outcomes. This work represents a component of her PhD work at Bournemouth University on modelling invasion dynamics to inform management programmes. She and the other authors collaborate on questions of invasive dispersal dynamics of freshwater fish at Bournemouth University and the University of Aberdeen.

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SUPPORTING INFORMATION

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