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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Speed and directedness predict colonization sequence post-disturbance

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Abstract

Foundational ecological models characterize dispersal with two behavioral traits, speed and directional bias. We hypothesized that these two traits can predict the order of colonization by fishes in a heterogenous landscape. Colonization patterns following hydrological disturbance were documented from a 20-year multi-site time series of marsh fish, and we evaluated the ability of a two-parameter model to predict these patterns. The maximum aerobic swimming speed (U_{CRIT}) for six coexisting fish species were estimated using endurance tests; field estimates of directedness and swimming speed were previously documented using encounter samplers. We incorporated interspecific variation in speed, direction, and density into several Agent Based Models to simulate dispersal following disturbance. Six virtual "species" with varying levels of directedness, "swam" in an artificial environment to reach a refuge habitat. The time of first arrival for each species was saved at the end of each run and used to calculate the probability of arrival order. Our simulated results generated predictions on order of arrival consistent with observed colonization patterns in our long-term dataset. Swim tunnel results revealed that fast (high U_{CRIT}) estimates were characteristic of early colonizing species; whereas, slow (low U_{CRIT}) estimates were characteristic of late colonizing species. Directional bias better predicted order of arrival than speed and was robust to inter-specific variation in density. This study demonstrated that two parameters were adequate to predict the order of species colonization in a complex landscape. These results support the use of relatively simple trait-based models to generate realistic community assembly dynamics.

Keywords Critical swimming speed · Diffusion model · Dispersal · Functional traits · Primary succession · Wetland

Introduction

The order of species arrival post-disturbance (sequential colonization) is hypothesized to be a critical factor in successional dynamics following intense disturbance (Spiller et al. 2018). Sequential colonization can lead to priority effects that provide a competitive advantage to early colonizing species over later ones (Symons and Arnott 2014). Early arrivals may block or inhibit colonization of later arriving species by monopolizing newly available resources (Fraser et al. 2015; Fukami 2015). Although strong dispersal potential is believed to cause these priority effects (Waters et al. 2013), trait-based studies investigating the key traits leading to sequential colonization and early arrival following disturbance are, however, lacking.

Ecological studies classify movement into three modes: passive; diffusive; and directed (Possingham and Roughgarden 1990; Tilman and Kareiva 1997). Passive movement, the spread of organisms by means of outside forces, characterizes displacement by stochastic processes such as currents or winds (Okubo 1994). Diffusive spread and random walks describe non-directional organismal movement through a landscape (Skellam 1951; Reynolds and Rhodes 2009). Movement is characterized as a series of 'steps' when

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the animal displaces itself in a unitary direction and speed before beginning a new step at a randomly selected angle from the previous one (Supplemental Appendix A). Some random dispersal models, such as Levy flights, vary step lengths by varying time traveled in the step at a constant rate or by varying movement rate at a constant time in the step (Viswanathan 2010). Finally, organisms display directed movement, or taxis, by responding to environmental cues and moving directionally in response to stimuli (Armsworth and Roughgarden 2005). Although evidence for directed movement is increasing (Nams 2006; Goss et al. 2014; Hoch et al. 2015), much of our understanding of the implications of movement on ecological dynamics is based on random movement of various forms (Méndez et al. 2016).

Functional trait-based mechanistic models have gained interest as tools to improve predictions of community composition and diversity (Cadotte et al. 2015). Foundational ecological models identified two traits to describe movement, directional bias (directedness or turning angle) and speed (Fisher 1937; Skellam 1951), but no study has investigated if these two historically modeled traits are adequate to describe animal dispersal and colonization order in nature as it relates to community assembly. Most studies rely on the comparison of step length distributions to those predicted by models such as Levy flights (Viswanathan 2010) creating a need for trait-based mechanistic analyses of movement patterns in field conditions (Hays et al. 2016). Species persistence in fluctuating environments may be dependent on their mode of dispersal (Johst et al. 2002), yet studies seldom quantify dispersal-specific traits for assemblages of coexisting organisms.

Functional variation in dispersal traits plays a central role in some theoretical depictions of metacommunity dynamics and spatial partitioning of biodiversity (e.g., dispersal-competition trade-offs in patch dynamics models: Leibold and Chase 2017). The relative mix of species with random and directed movement may maintain biodiversity since random movement supports both γ and α diversity, while directed movement tends to support β diversity via local coexistence and niche partitioning, respectively (Armsworth and Roughgarden 2005). It is still unclear how interspecific variation in movement strategies influences the rates at which species colonize newly available habitats and their role in early successional dynamics beyond a theoretical context (Cote et al. 2017; Jeltsch et al. 2013). We are aware of no animal study (but for plants, see Campbell et al. 2003) that has directly described or linked the range of movement traits in a regional pool of species to colonization rates for a collection of coexisting species post-disturbance.

In this paper, we explore the predictive power of information on species' dispersal traits in a field setting with extensive time-series data on community reformation following disturbance. We developed a framework to determine how interspecific variation in movement traits relate to colonization success by screening a group of co-existing species for their speed (maximum critical swimming speed) and directedness. This study coupled functional analyses of swimming performance with a simple model to predict the order of species re-colonization of sites following disturbance. We then evaluated those predictions with a 20-year dataset on recolonization patterns in a complex floodplain ecosystem, the Everglades of Florida, USA.

Methods

Study site and species

The freshwater marshes of the Florida Everglades experience seasonal rainfall patterns with an annual dry (November–April) and wet (June–September) period (Ogden et al. 2005), with seasonal inundation a direct result of rainfall and recession caused by drainage and evaporation of surface water (Fennema et al. 1994). The persistence of fish communities in these landscapes is facilitated by the hydrologic connectivity between permanent and ephemeral habitats. This results in temporal shifts of fish densities, causing these organisms to immigrate in with flooding or emigrate out when drying or face desiccation (Trexler et al. 2011). Furthermore, flow velocity is consistently low (< 3 cm s^{-1}) (Larsen et al. 2011) and colonization following inundation is driven primarily by changes in movement behaviors (Goss et al. 2014; Hoch et al. 2015).

From 1996 and 2016, we collected fish using a 1-m^2, 2-mm mesh, throw trap following a standard protocol (Jordan et al. 1997) at 21 monitoring sites in the Everglades, Florida, USA (Supplemental Appendix B). Six sites were in Shark River Slough (SRS), five in Taylor Slough (TSL), and 10 in Water Conservation Areas (WCA) 3A and 3B. Samples were collected at each site in five months of each year (July, October, December, February, and April) to characterize a 'water year' from the wet season (begins in June) to dry season (begins November). Each site consisted of three plots, except for short-hydroperiod sites in TSL (MDsh and TSsh), which had two plots each. Five (WCA 3A and 3B) or seven (SRS, TSL) throw trap samples were collected within each. Plots located in WCA 3A and 3B yielded 25 samples per year (5 throws × 5 sample events), while plots in SRS and TSL yielded 35 samples per water-year (7 throws per plot × 5 sample events). Throw locations within each plot were determined using a random number table. After securing the trap, floating vegetation (non-rooted vascular plants and periphyton mat) was quantified and cleared before fish were removed following a standardized protocol of sweeps with a bar seine and dip nets. Vertebrate organisms were euthanized using a solution of MS-222 and ambient marsh water (Nickum et al. 2004). There is no evidence of visitor impact on these long-term study sites, possibly because marsh plants re-grow quickly and periodic marsh drying overwhelms sampler impacts on vegetation and soil (Wolski et al. 2004). Additional information on the study sites and sampling design are described in detail in other publications (Trexler et al. 2002, 2003, 2005).

This study focused on the six most abundant marsh fish species at all study sites. These include three members of the Poeciliidae: *Gambusia holbrooki* (Eastern Mosquitofish), *Heterandria formosa* (Least Killifish), and *Poecilia latipinna* (Sailfin Molly), two members of the Fundulidae: *Lucania goodei* (Bluefin Killifish) and *Fundulus chrysotus* (Golden Topminnow), and one member of the Cyprinodontidae: *Jordanella floridae* (Flagfish). These species can be further classified based on three distinctive life history strategies related to recovery following drought: rapid recovery and sustained high density (*G. holbrooki*), rapid recovery followed by a decline in density (*J. floridae*, *F. chrysotus*), and slow recovery over time (*L. goodei*, *H. formosa*, *P. latipinna*). These have been described in detail in other publications (DeAngelis et al. 2005; Trexler et al. 2005). Furthermore, the relative importance of local reproduction in recovery patterns of these populations in response to drought is poorly understood, but cannot explain some of the previously discussed patterns of density increase following droughts (Goss et al. 2014). Populations from small, local refuges (alligator holes) sustain population sizes that are far too low to explain re-colonization (Loftus et al. 1992; Gaff et al. 2000; Kobza et al. 2004). Results from simulation models suggest that directed movement from large, permanent water bodies is needed to supply the biomass observed following inundation (DeAngelis et al. 2010; Jopp et al. 2010). Therefore, differences in colonization potential among these six species is believed to be primarily by movement behavior leading to immigration and not local reproduction.

Colonization patterns

We analyzed a 20-year time-series dataset to determine the colonization patterns following re-inundation at 21 long-term monitoring sites. To determine when a habitat became re-inundated, hydrology data were extracted from the Everglades Depth Estimation Network (EDEN). EDEN uses water-surface models to interpolate measured water depths at monitored gauges to estimate daily water depth at our study sites (Telis 2006; Liu et al. 2009). We used these data to create a count variable, days since the site was last dry (DSD), which records the cumulative number of days since gauges last recorded a water depth < 5 cm for each sampling event. At 5 cm, only a slurry of organic matter remains, and fish generally suffocate in the low oxygen conditions and organic matter blocking their gills. We used plot-level data as replicates. All data collected at a plot prior to the first detectable drying event were not considered because colonization time could not be estimated. Plots lacking a disturbance event were also excluded from our analyses. We then determined all samples that were collected between disturbance events and recorded the presence or absence of each species in these samples. Using temporal tabulations of species presence (count > 0) or absence (count $= 0$), we recorded the cumulative number of sample periods that each species was absent prior to first detection following marsh re-flooding.

We hypothesized that the time to re-colonize a site would influence a species' abundance following drought. To test this hypothesis, we calculated three metrics of density: density at first arrival post-drought, average density while inundated, and maximum density while inundated. Densities were calculated using the abundance of fish in each of the 5–7 1-m^2 throw-trap samples while sites were inundated. We first determined the initial density of fish (density at first arrival) by calculating the density when each species was initially collected following inundation. Mean density while inundated was calculated by averaging the densities for all samples collected between successive drying events. Furthermore, we determined the peak density during inundation to determine if early colonization was related to increased population size (maximum density while inundated) post-inundation. Spearman's rho, a nonparametric correlation, was used to document the relationship of recolonization patterns and density metrics. For statistical analyses, a species was assigned a colonization time equal to the maximum number of samples collected following a disturbance when no specimens of the species were collected. Rankings were assigned based on the first instance of appearance and were ranked equally if they arrived simultaneously. This ensured that these species received the earliest arrival rank possible, even when accounting for ties. Spearman's rho was calculated separately for each drying event using the rank order of arrival time and each metric of density (density at first arrival post-inundation, average density, maximum density). We then used a general linear model (GLM) to test the main effects of arrival order and species on average density. Average density was log-transformed to meet the assumption of normality. Each plot was analyzed separately with replication within a plot being individual drying events (2–20 drying events per plot). Plots that lacked a drying event or experienced only one drying event were excluded from analyses due to lack of replication. These, and all other analyses, were conducted using SAS 9.4 (Insititute 2012).

We also determined arrival order at each site by species for each drying event. We ranked each species' arrival time (earliest $= 1$, latest $= 6$) and addressed ties by assigning the lowest rank for all species with the same arrival time; ties occurred when species first arrived at the same sample event. To avoid fractional orders of arrival, a rank of 1 was associated with all species that arrived first to ensure a range of whole numbers from 1 to 6. We then used these ranks to calculate arrival probabilities, or the proportion of drying events where a species arrived at each arrival order, for each species by using the following formula:

$$p_i = \frac{X_i}{n}, \tag{1}$$

where p_i is the probability of arrival, X_i is the number of drying events where a species arrived in the *i*th order, and n is the number of drying events in the time series.

Quantifying swimming speed

We estimated critical swimming speed (U_{CRIT}), or the maximum sustained aerobic speed, as a metric of fish swimming ability (Plaut 2001). We hypothesized that the maximum aerobic speed would be physiologically limiting and one species-specific aspect of colonization potential. To investigate interspecific variation in U_{CRIT}, adult and juvenile fish for each species were collected from the Everglades using a dip net and transported to an indoor wet lab at Florida International University, Miami, FL, USA. All fish were housed in 75.7-l aquaria under a 12/12 photoperiod. Individuals were fed Tetramin® once daily prior to each trial. Species were allowed 3–4 days to recover from stress caused by transport and transplantation into laboratory aquaria. Individual fish were then placed in a Blazka-style swim chamber (Blazka et al. 1960) and allowed to acclimate at low-flow speeds (2–6 cm s^{-1} or 1–3 BL s^{-1}) for 30 min to induce rheotaxis. Following the acclimation period, flow velocity was increased by 2 cm s^{-1} every 5 min until the individual could no longer swim against the current and was swept backward onto the meshed end of the chamber. Fatigue was assessed when an individual could no longer maintain its position against the flow and did not respond to stimulation for three consecutive attempts. Aeration was placed at the downstream end of the flume to ensure that the water was properly oxygenated and not a limiting factor during each trial. All swimming trials were conducted between 23 and 26 °C. Both the final velocity and the time until exhaustion at the final velocity were recorded. The critical swimming speed was then calculated using the following formula:

$$U_{\mathrm{CRIT}} = U + \left[U_i \times \left(t/t_i\right)\right], \tag{2}$$

where U_i is the velocity increment (2 cm s^{-1}), t_i is the time increment (5 min), U is the final velocity a fish swum for the full 5 min, and t is the time swum at the final velocity (Plaut 2001).

The critical swimming speed was evaluated for 20 juveniles and 20 adults of varying lengths (approximately one individual per mm in length) of each species ($n = 40$ per species). The size range selected for each species was based on the observed size range of specimens within the 20-year time series. Time in captivity and time since last feeding were also assessed to determine any influence that these variables may have on estimated critical swimming speed. Furthermore, no fish that were housed for more than 12 days were used to prevent domestication of housing and feeding conditions. We used an ANOVA to evaluate differences in species' swimming ability. A post-hoc Tukey's pairwise comparison was used to group each species into high, moderate, or low dispersal capacity based on their respective U_{CRIT}. Furthermore, we used absolute speed (cm s^{-1}), not relative speed (body lengths per second, BL s^{-1}), for our analyses since the objective was to determine which species would arrive first based on speed. Spearman's rho was then used to test the correlation between both laboratory and field estimates of speed.

Agent based models to simulate dispersal

Our initial results on fish swimming performance revealed that absolute speed was insufficient at describing species' arrival order. Previous studies have indicated that these species vary in their level of directedness in response to changing hydrology (Goss et al. 2014). These estimates were derived using encounter samplers placed during times of rising and falling water levels. Each encounter sampler consisted of drift fences with four minnow traps installed at right angles. The four traps were placed to face the four cardinal directions (North, South, East, West) and left for 24 h. The total number of individuals caught per species was treated as the magnitude of a vector, with the direction oriented in the direction of the trap. These vectors were averaged, and the magnitude of this averaged vector was treated as "bias". Non-directional movement was determined if the magnitude of the four vectors did not differ among the four traps. A more detailed description of the drift fence design and analyses determining directional bias can be found in selected publications (Obaza et al. 2011; Hoch et al. 2015).

ABM's were implemented in Netlogo 5.3.1 (Wilensky 1999) and the following model description follows the ODD (overview, design concepts and details) protocol. A complete summary of the ABM's design can also be found in Table 1.

Purpose

The purpose of these models was to test the interaction between speed and directedness on species' arrival order and time to colonization post-inundation. The ABM's were designed to simulate the seasonal flooding of Everglades

Table 1 Description and overview of the agent-based models

Element	Description
Agents	Six fish species with varying levels of directedness (Table 1)
State variables	Speed (cm/s) Distance from refuge habitat (m)
Scale	
Spatial	1 Grid = 10 × 10 m Size: 2000 × 1760 m (3.52 km^2)
Temporal	1 unit time = 1 s Duration: 12 h (43,200 time steps)
Environment	Refuge habitat 1000 m north stops movement
Process overview and scheduling	Turn Move forward Repeat until at refuge habitat or t = 43,2001
Basic principles	Passive diffusion, dispersal, recolonization
Emergence	Arrival order Probability or arrival
Objectives	Reach refuge habitat located 1000 m north of initial habitat
Stochasticity	Original orientation (random within 360°) Turn: normal distribution ($\mu = 0$, $\sigma = 10$) Move forward: exponential distribution (μ)
Observation	Time of arrival (s) Distance from refuge habitat (m)
Initialization	Clear environment Generate refuge habitat Generate initiate habitat 1 km due south Generate 600 agents (6 species, 100 per species) Assign random heading to each agent Set $t = 0$
Input data	Speed (see "Results") Directedness (Hoch et al. 2015) Turning angle (Domenici and Blake 1997)

marshes and the different movement patterns associated with the colonization of six common marsh fish species. We created virtual fish species to swim in our artificial marsh habitat to simulate the movement of individual fish in a marsh that is drying.

State variables and scale

Agents within our models represent a community of six coexisting fish species within the Florida Everglades. Six virtual fish species, each with varying levels of directedness, were designed to represent one of the six fish within our field and laboratory studies. This virtual environment was scaled to the speeds estimated from our swimming performance study to simulate long-distance dispersal of these fish (Baber et al. 2002; Hohausová et al. 2010). One grid cell was equivalent to 10 × 10 m and the model landscape comprised 2000 × 1760 m (3.52 km^2) of fully connected, homogeneous environment. Homogeneity was designed to avoid the complexity that would be posed by a variety of habitat types and preferences. Further, we assigned coordinates in our world to correspond to the cardinal plane (North = 0°, East = 90°, South = 180°, and West = 270°). Our ABM's were scaled to a temporal scale of one-time step equaling one second in real time. Each simulation ran for 12 h (43,200 time-steps) to correspond to a 12/12 photoperiod or a day's worth of active movement. A refuge habitat was located 1-km north of the initial habitat (Fig. 1). The edges of the model were not wrapped vertically or horizontally, and individuals were free to move outside the model landscape. Edge effects were eliminated since the x-coordinates for the refuge habitat was not bounded [$-\infty$, ∞]. Individuals could still reach the refuge habitat while outside the model landscape.

Process overview and scheduling

Every time step, the speed and orientation of an individual was updated according to the assigned average speed and directedness. Individuals re-oriented themselves and moved forward based on the randomly assigned values from the submodels. Agents swam continuously for the 12-h simulation or until they reached the refuge habitat. Individuals who reached the refuge habitat were instructed to stop motion until the end of the simulation.

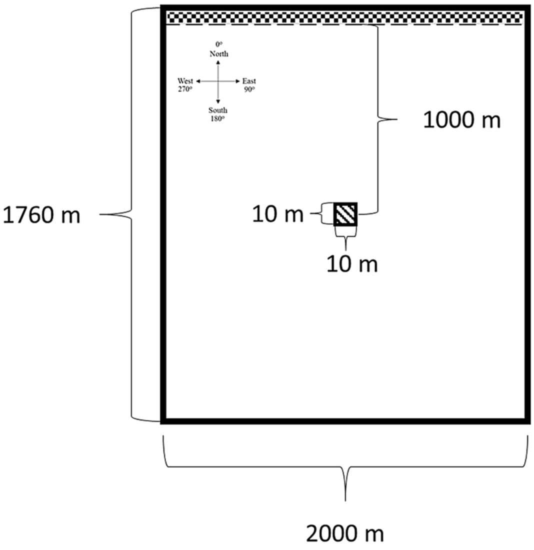

Fig. 1 A visual representation of the virtual world for agent-based models created in Netlogo. The original habitat (striped region) is located 1000 m due south of refuge habitat (checkered region)

Design concepts

Both speed and directional bias are important components of species dispersal models (Skellam 1951). To investigate the effects of both swimming speed and direction on dispersal potential, we created a series of ABM's (Grimm et al. 2006) that incorporated both our laboratory estimates of speed and previously described estimates of directedness. Furthermore, the least directed individual was created to represent the standard passive diffusion model (Skellam 1951). Summary statistics (mean, minimum, maximum, standard deviation) for the time at first arrival of each species were collected at the end of each run. The spatial distribution for each species was also observed by calculating the distance from the refuge habitat for each agent following each simulation. Stochasticity was assumed in the random-number generators in our speed, turning angles, and initial headings and each scenario was replicated 10 times.

Initialization

Each ABM was initialized by first clearing the environment of all agents and habitats. Simulations were reset ($t = 0$) and both the refuge habitat and initial habitat were generated prior to placing agents within the environment. Agents were then placed within the newly constructed environment in an artificial habitat (100 m^2, 10 m × 10 m) located 1-km south of the refuge habitat (goal of simulation). We used 1 km because this is the average distance between plots at our long-term study sites. We simulated 100 individuals per species within this habitat to produce a density of 1-individual per m^2 and assigned a random heading. This produced a total of 600 agents per simulation. Density was standardized to reflect only changes in speed and directedness since field results indicated colonization time was independent of density. We also conducted two trials where the density of each species was manipulated. One trial used randomized densities and the other used fixed densities that decreased with increasing directedness (Supplemental Appendix C).

Input

The model included speed data (present study) and directedness data from Hoch et al. (2015).

Submodels

Movement based on speed and directedness was described using a series of submodels within our simulations. The first three submodels corresponded to the directedness of an individual agent by manipulating its orientation and turning angel respectively. Directedness was categorized by restricting the heading of each species outside of

$$\left[a^\circ, b^\circ\right],$$

where a° and b° are coordinates in the cardinal plane. This reduced the range of motion for each of the six species to 180° (most directed), 225°, 270°, 315°, 330°, and 360° (least directed) respectively. The bounded range of the restricted region for each species is provided in Table 2. Individuals were programmed to re-orient themselves within the opposite direction of the restricted region if their randomly assigned heading was within the bounded region by a series of conditional statements:

$$\text{If Heading} = a^\circ \text{ then Heading} = a^\circ - [1, 20],$$

$$\text{If Heading} = b^\circ \text{ then Heading} = b^\circ + [1, 20],$$

where a° and b° are coordinates within the restricted orientation and [1, 20] are numbers selected from a random number generator bounded between 1 and 20. An angle of 20° was selected because it corresponds with the maximum turning angle that fish can maintain within a 1-s period (Domenici and Blake 1997).

The next submodel, turning angel, assigned a turning angel at each time increment prior to moving forward. This was randomly assigned to each agent based on:

$$\text{Turning Angle} \sim N(0, 10),$$

where right turns corresponded to positive values and left turns corresponded to negative values of this distribution.

Table 2 Restrictions and characteristics of the six virtual species (agents) used in the agent based models

Species	Restricted orientations	Range of motion	Movement type
Species 1	No restriction	360°	Passive diffusion
Species 2	[165°, 195°]	330°	Cannot move due south
Species 3	[157.5°, 202.5°]	315°	Slightly directional
Species 4	[135°, 225°]	270°	Increased directedness; cannot move between SW and SE
Species 5	[112.5°, 247.5°]	225°	Highly directional
Species 6	[90°, 270°]	180°	Highly directional; no southern heading

Restrictions on orientation were used to produce varying levels of directedness

Therefore, a turning angle of − 10 corresponds to the fish turning left ten degrees.

Our final submodel described the speed of each individual agent by assigning a distance to move forward based on the folowing:

$$\text{Speed} \sim \exp(1/\mu),$$

where μ is the mean of the exponential distribution. We specifically tested speeds in 3 cm s^{-1} increments ($\mu = 9$, 12, 15, 18, 21, and 24 cm s^{-1}) based on interspecific variation in U_{CRIT} derived from this study. The exponential distribution was selected because of its resemblance to prolonged swimming speed curves (Fisher and Bellwood 2002). Netlogo's program BehaviorSpace was used to model every speed/directionality combination (six speeds, six levels of directedness, 6^6 or 46,656 simulations). A total of 466,560 runs were conducted following replication of each scenario.

Validation of agent based models

Following all model simulations, we validated our ABM's by comparing field estimates to those generated in our models. First, we described each of the six species based on their response to changing hydrology. We considered arrival order (present study), estimates of latency time/activity level (Hoch et al. 2019), and magnitude of directional bias (Hoch et al. 2015). We arranged species in the following order: *J. floridae* (most directed/earliest colonizer), *G. holbrooki*, *F. chrysotus*, *L. goodei*, *H. formosa*, and *P. latipinna* (least directed, late colonizer). Both *G. holbrooki* and *J. floridae* had similar estimates for all categories considered so field estimates of arrival order described in this study took precedent. For our ABM's, species were arranged based on their level of directedness (most to least directed). This would compare *J. floridae* to Species 6 in our ABM's following a descending order of directedness to compare *P. latipinna* to Species 1 (least directed).

We averaged the time at first arrival for the 10 replicates, then ranked the arrival time in descending order (1 = first to arrive, 6 = last to arrive). Each rank was turned into an arrival probability by determining the proportion of simulated runs that a species arrived in a particular order using Eq. 1. Arrival probabilities from our ABM's were then compared to the arrival probabilities estimated from our field data. We calculated Kendall's Tau (τ), a nonparametric correlation test, to compare the arrival probabilities between our observed and simulated data. We considered significance at both $\alpha = 0.05$ and $\alpha = 0.10$ to account for the small sample size in these comparisons ($n = 6$). Both interspecific variation (rows) and intraspecific variation (columns) were compared using Kendall's Tau. We also compared the average arrival order for our species in the field to the arrival order of each species in our simulated data. Results from our density ABMs were compared to our field results to determine if differences in species density within our models altered the results.

Results

Colonization patterns

Our analysis revealed 536 drying events at 51 plots throughout the 20 years of this study (0–19 disturbance events per plot). Seven plots experienced no drying events and were removed from further analyses. Of the 536 drying events, > 70% of observed recolonizations were uncorrelated with the species' density, regardless of the density metric used. These results revealed that early colonization did not lead to higher density for any species (Fig. 2a–d). Our GLM's further analyzed arrival order on average density for 46 of the 51 plots. Five plots were removed due to inadequate replication (1 drying event per plot). These analyses determined that arrival order did not significantly influence species density post-inundation for 57% of plots. Furthermore, the GLMs revealed that density had a larger effect on arrival order as plots became more frequently disturbed (Table 3).

The rank of inter-specific arrivals at re-inundated plots was highly repeatable (Table 4). Three species (*L. goodei*, *H. formosa*, *P. latipinna*) consistently recovered slowly

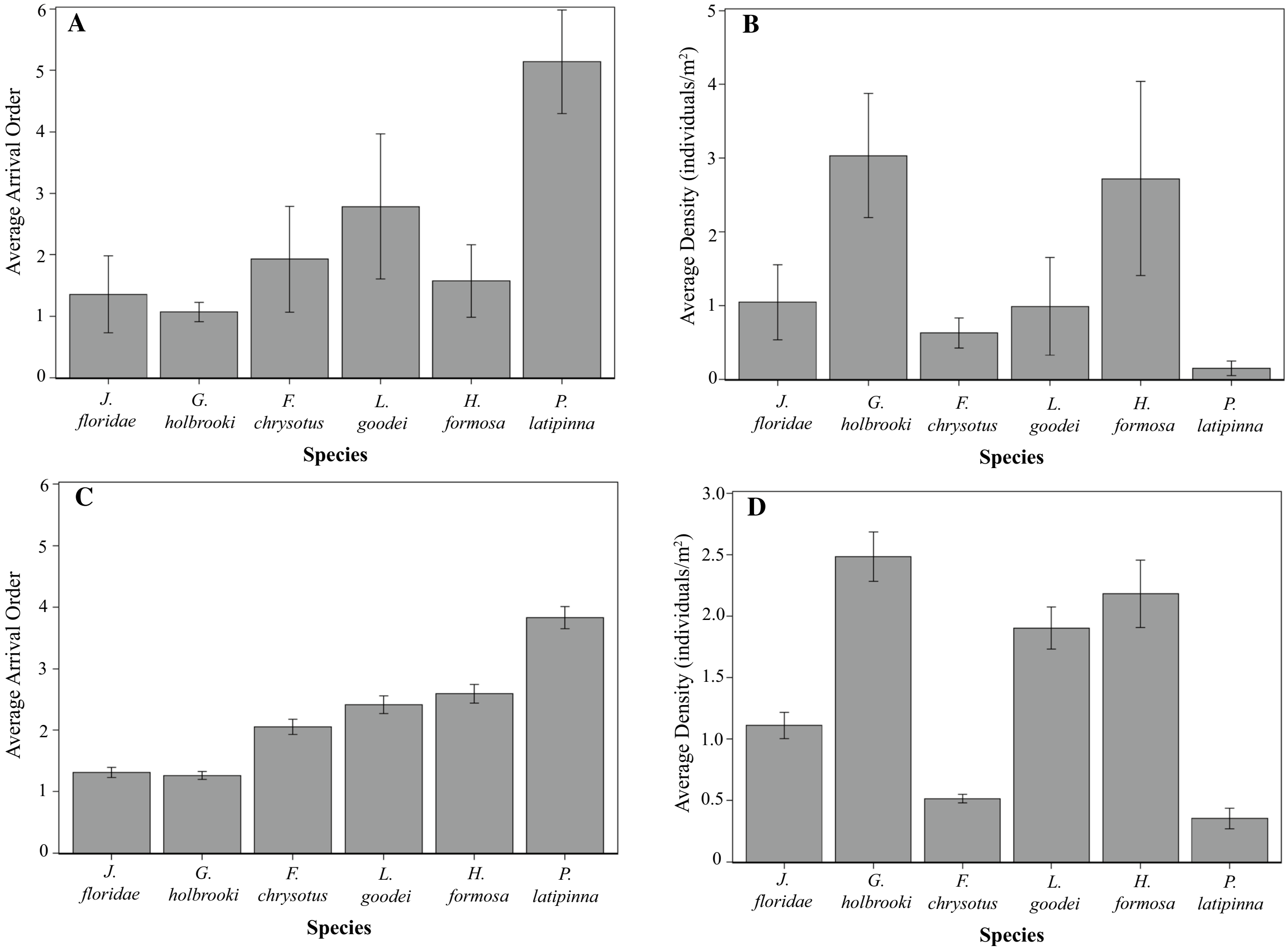

Fig. 2 Top row: **a** the average arrival order across flooding events and **b** average density while inundated of each species at a representative study plot (WCA Site 10, Plot A; mean ± 95% CI are plotted). Bottom row: **c** the average arrival order of each species and **d** the average density while inundated. These averages were calculated across all flooding events within plots, then across plots within sites, and then among sites (mean ± 95% CI are plotted). In all graphs, the *x*-axis is arranged from average earliest arrival to latest and is standardized to compare arrival and density metrics

Table 3 Summary of GLM's used to test the main effects of arrival order and species on average density

Main effect	Short		Intermediate		Long		Overall	
	$p<0.05$	$p\geq0.05$	$p<0.05$	$p\geq0.05$	$p<0.05$	$p\geq0.05$	$p<0.05$	$p\geq0.05$
Arrival	8 (62%)	5 (38%)	12 (40%)	18 (60%)	0 (0%)	3 (100%)	20 (43%)	26 (57%)
Species	11 (85%)	2 (15%)	26 (87%)	4 (13%)	0 (0%)	3 (100%)	37 (80%)	9 (20%)

Values indicate the number of plots where the main effect was either a significant or not significant. Parentheses indicate the proportion of those plots. Plots were divided into long (<4 drying events in 20 years), intermediate (4–12 drying events in 20 years), and short-hydroperiod sites (>12 drying in 20 years)

following disturbance and often required multiple sampling events post re-flooding before they re-appeared. In contrast, this was rare for early colonizing species (*G. holbrooki*, *J. floridae*, *F. chrysotus*), which regularly returned in a few weeks post-disturbance. Our GLM's also indicated that arrival order was different among species; however, these differences became less clear at plots that experienced very little disturbance.

Table 4 Arrival probabilities for each species ($n = 536$) estimated from field data collected post-disturbance (± 95% CI)

Arrival order	Species					
	J. floridae	*G. holbrooki*	*F. chrysotus*	*L. goodei*	*H. formosa*	*P. latipinna*
1st	0.88 (0.03)	0.87 (0.03)	0.59 (0.04)	0.52 (0.04)	0.50 (0.04)	0.28 (0.04)
2nd	0.04 (0.01)	0.04 (0.02)	0.06 (0.02)	0.05 (0.02)	0.03 (0.01)	0.01 (0.01)
3rd	0.02 (0.01)	0.06 (0.02)	0.13 (0.03)	0.11 (0.03)	0.07 (0.02)	0.06 (0.02)
4th	0.02 (0.01)	0.03 (0.01)	0.11 (0.03)	0.12 (0.03)	0.14 (0.03)	0.09 (0.02)
5th	0.04 (0.02)	<0.01	0.08 (0.02)	0.12 (0.03)	0.20 (0.03)	0.17 (0.03)
6th	<0.01	<0.01	0.03 (0.01)	0.08 (0.02)	0.06 (0.02)	0.39 (0.04)

Some species arrived at the same sample event and were assigned the same ranks; probabilities were calculated by species, so columns but not rows sum to one

Quantifying swimming speed

Our analyses revealed that subtle differences in prolonged swimming speed were enough to differentiate species based on their speed/endurance in our swimming performance tests. Our ANOVA model revealed these differences in swimming speed (4–6 cm s^{-1} between groups) to be significantly different ($F_{5,234} = 20$, $p < 0.001$). A post hoc Tukey test using pairwise comparisons revealed three distinctive swimming speed groups in the six species (Fig. 3). Three species (*G. holbrooki*, *J. floridae*, *F. chrysotus*) had faster/higher endurance ($U_{CRIT} >= 19$ cm s^{-1}) than the other three species; whereas, two species (*L. goodei*, *H. formosa*) had the lowest speed/endurance ($U_{CRIT} <= 13$ cm/s). One species, *P. latipinna*, had speed/endurance estimates that were similar to both *F. chrysotus* and *H. formosa*, indicating an intermediate species with moderate speed/endurance (19 cm s$^{-1} > U_{CRIT} > 13$ cm s^{-1}). Furthermore, our estimates of U_{CRIT} were consistent (Mean Difference: 10.13 ± 3.26) with indirect estimates in the field using encounter samplers (Table 5). This revealed that individuals with high U_{CRIT} estimates also had high indirect measures of speed estimated in the field, though U_{CRIT} estimates were generally higher. However, laboratory estimates of swimming speed were not correlated with indirect measurements of swimming speed in the field ($r_s = 0.5$, $p = 0.391$). Analyses also revealed that interspecific differences in swimming speed were not influenced by our housing or feeding conditions.

Model testing and validation

Our ABM's simulated over 466,560 different artificial disturbance events and produced arrival probabilities based on different speed/directedness combinations. The outcomes revealed that faster, more directed individuals were more likely to reach a habitat first compared to slower, non-directed ones. The fastest/most directed individuals were the first to arrive; whereas, the slowest/least-directed individuals were among the last. Although our simulations revealed that the most directed individuals were most likely

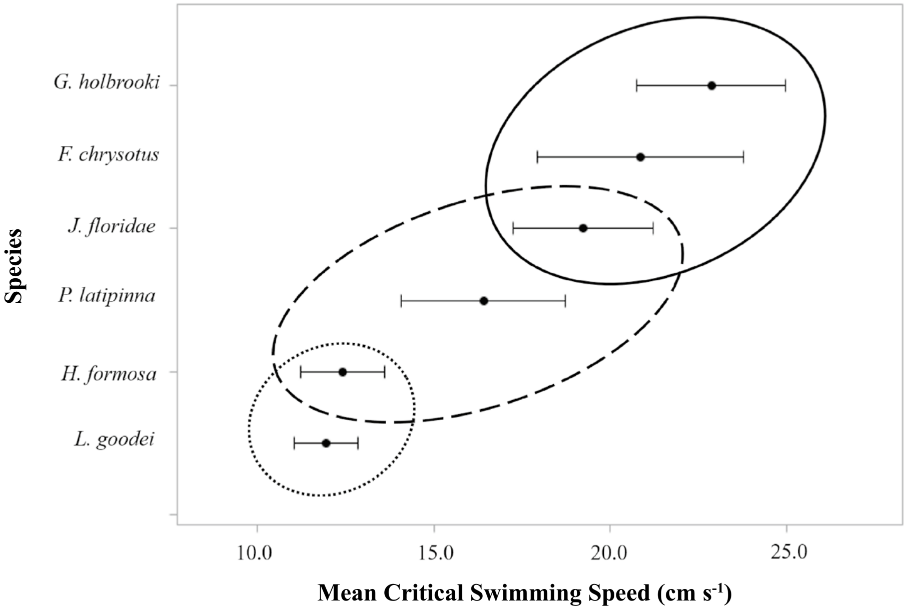

Fig. 3 Results of ANOVA with Tukey's Pairwise Comparisons on interspecific variation in U_{CRIT}. Three distinct groups were detected (fast, intermediate, slow) and are indicated by the enclosure of the means in ellipses

Table 5 Comparison of species dispersal characteristics from both laboratory and field studies

Species	Arrival order	Direct estimate of speed (cm s^{-1})	Field estimate of speed (cm s^{-1})	Observed directedness
G. holbrooki	1st/2nd	22.86 ± 1.05	9.75 ± 1.21	Directed
J. floridae	1st/2nd	19.23 ± 0.97	13.25 ± 2.13	Directed
F. chrysotus	3rd	20.85 ± 1.45	6.13 ± 0.74	Directed
L. goodei	4th	11.94 ± 0.45	3.82 ± 0.61	Directed
H. formosa	5th	12.39 ± 0.59	N/A	Undirected
P. latipinna	6th	16.40 ± 1.15	7.66 ± 1.55	Undirected

Direct estimates of speed were calculated following endurance tests (mean ± SE). Field measures of speed (mean ± SE) were estimated using encounter samplers (Bush 2017). Observed directedness was taken from Hoch et al (2015)

Table 6 Arrival probabilities for each species of simulated dispersal using agent based models and Kendall's Rank Correlation Coefficient (τ)

Arrival order	Species						
	Species 6	Species 5	Species 4	Species 3	Species 2	Species 1	Kendall's Tau (τ)
1st	0.65	0.28	0.07	<0.01	0.00	0.00	0.89**
2nd	0.24	0.43	0.27	0.05	0.01	<0.01	0.55
3rd	0.10	0.19	0.42	0.26	0.17	0.09	0.69*
4th	0.01	0.07	0.18	0.50	0.49	0.38	0.73*
5th	0.00	0.03	0.06	0.18	0.31	0.41	0.73*
6th	0.00	<0.01	<0.01	0.01	0.02	0.12	0.77*
Column τ	0.59	0.69*	0.33	0.00	0.20	0.28	

Species are arranged left to right by decreasing levels of directedness. Results for each species includes each speed tested. Some species arrived at the same sample event and were assigned the same ranks; therefore, only column values will sum to one. Kendall's Tau was calculated based on comparing values in the same row and columns (arrival order) from Table 2. Two asterisks (**) indicate significance at $\alpha = 0.05$ and single asterisk (*) indicates significance at $\alpha = 0.10$

to arrive earlier, traveling at slower speeds hindered their overall colonization time. Interspecific trends (rows) in simulated arrival probabilities (Table 6) were highly correlated ($\tau = 0.55$–0.89, mean $\tau = 0.73^{\pm}0.05$) with observed species arrival probabilities from field data; however, intraspecific trends (columns) in arrival probabilities were weakly correlated (Table 4). Overall, the arrival probabilities calculated from both our field data and ABM's were moderately correlated ($\tau = 0.31$, $p < 0.05$). Species' arrival order was highly correlated with species' arrival order in the simulated data ($\tau = 0.87$, $p < 0.05$).

We did not detect effects of density on our ABM results. Both ABMs designed to validate our colonization-density results produced arrival probabilities that did not differ from our original results when using either fixed (see Supplemental Appendix C, Table C.1) or randomized densities (see Supplemental Appendix C, Table C.2).

Ecological applications

Our ABMs revealed that reduced speed and/or directedness hindered a species' overall colonization time. Model results revealed changes in arrival order between the fastest/most directed individuals (first), slower/less directed individuals (second through fourth), and the slowest/least directed individuals (fifth through sixth) post-disturbance (Fig. 4a–c). We detected a linear increase in the probability of arriving first with increasing speed; however, we observed a nonlinear increase in first arrival with increasing directedness (Fig. 5a). The models yielded a sigmoidal relationship between increasing direction in the proportion of individuals who successfully colonized (Fig. 5b) indicating that arrival is more sensitive to changes in directedness than to changes in speed. Increasing speed by 266% decreased the probability of arriving last from 0.03 to 0.02; whereas, increasing directedness by 180° decreased the probability of arriving last from 0.12 to zero. Similar trends were revealed for the probability of arriving fourth, decreasing from 0.39 to 0.20 (266% change in speed alone) and from 0.37 to 0.01 (180° change in directedness alone).

Discussion

Early attempts at modeling animal movement evaluated two traits in diffusion models: speed (distance and time moving in a direction) and turning angle. These theoretical models have been applied extensively when developing ecological

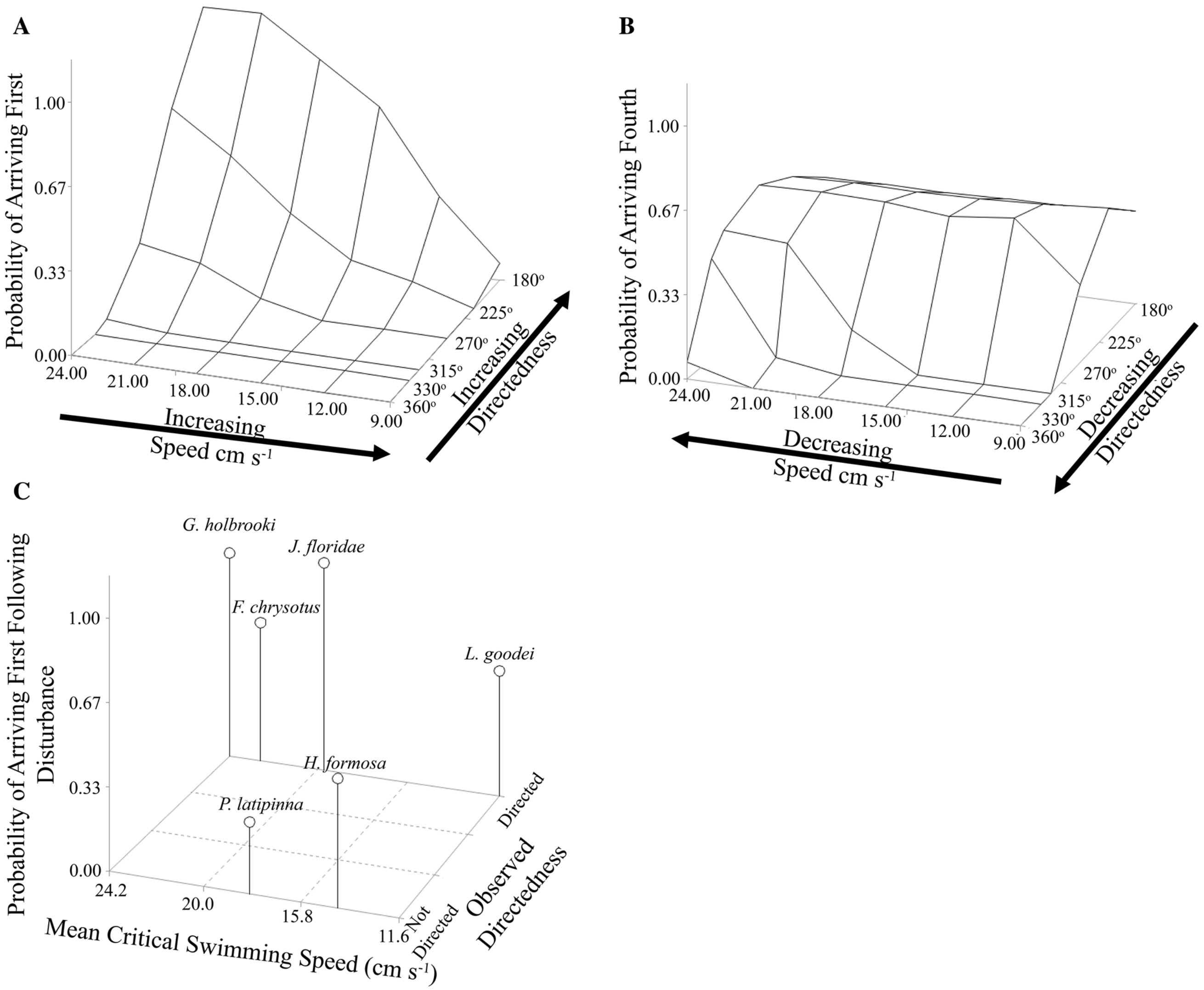

Fig. 4 Three-dimensional plot describing arrival probabilities based on speed/directedness combinations from the ABM's for **a** arriving first and **b** arriving fourth. The horizontal axes for Fig. 3b were rotated 180° to highlight differences between fast/directed and slow/non-directed. Arrival probabilities were calculated based on arrival time at the end of each simulated run. **c** Observed field probabilities of arriving first based on a species estimated U_{CRIT} and observed directedness in the field. U_{CRIT} was calculated from endurance tests. Directed species were assigned a value of 1 and non-directed species a value of 0. Observed field probabilities were calculated based on species' arrival times following re-inundation of the habitat (Table 2)

theory (DeAngelis et al. 2010), and we provide empirical evidence that post-disturbance colonization of fishes in a complex wetland can be predicted by these two movement parameters, speed and directedness. We found that speed and directedness, estimated independently for six fish species from field and laboratory studies, predicted the same order of recolonization following drought that was observed in a complex wetland over a 20-year period. Our results demonstrate that simple behavioral parameters from a theoretical model can be applied to field settings and parameterize a simple yet predictive model. The model permitted us to investigate the relative contribution of each movement parameter to both arrival order and recolonization success and suggested that directedness has a non-linear relationship with colonization success; increasing directedness had a greater impact on the probability of early arrival than increasing speed.

Species' composition and density within regional source pools plays a vital role in community assembly and colonization dynamics of disturbed patches (Stoll et al. 2014). We investigated the effects of arrival order on the establishment of species' populations. Those results indicated that arrival order had little to no effect on subsequent population size. We are not able to estimate the density of potential colonists in refuges before flooding because we currently are unable to track these small fishes in the field. However, we used

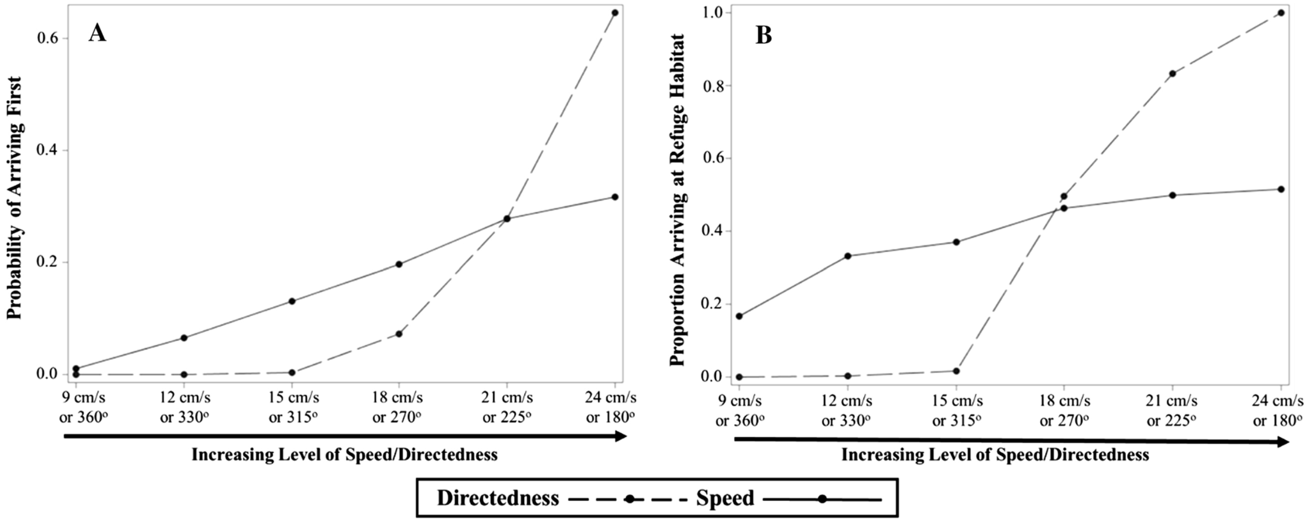

Fig. 5 Probability plots of two metrics of recolonization potential: Speed and directedness. The two extremes are designed to represent non-directed vs directed individuals. **a** The probability of arriving first based on a species' level of directedness (independent of speed) and speed (independent of directedness). **b** The proportion of each individual arriving at the refuge habitat after each run based on a species' level of directedness (independent of speed) and speed (independent of directedness)

our ABM's to investigate the hypothesis that the density of potential colonists influences arrival order. In simulations, we found no correlation of arrival order on density prior to flooding. Increasing refuge population size in our ABM's did enhance colonization success of non-directional species but had little effect on arrival order. These simulations suggest that directedness plays a more important role in colonization dynamics than population size within regional source pools. Further work is needed to understand the interactive effects of initial density, speed, and directedness on species' arrival order and community assembly processes.

Interspecific variation in movement types contributes to maintenance of biodiversity and community persistence in disturbed ecosystems (Johst et al. 2002; Armsworth and Roughgarden 2005). Chesson (2000) described trade-offs among life-history traits, including those related to dispersal, that promote coexistence of competing species in nonequilibrium communities. Our study provides a detailed evaluation of traits linked to dispersal by describing interspecific variation in physiology (speed/endurance) and behavior (directedness). Our ABM's suggest that increased directedness has a greater impact on colonization success than speed, which is consistent with our field data. For example, *L. goodei* had the lowest U_{CRIT} estimate of all species but colonizes a newly inundated habitat earlier than both *H. formosa* and *P. latipinna*. Previous studies have revealed that *L. goodei*, unlike *P. latipinna* and *H. formosa*, respond to environmental fluctuations with directionally biased movement (Goss et al. 2014; Hoch et al. 2015). This species' lack of speed was compensated by its ability to respond directionally to a changing environment and seems to enhance early arrival at newly inundated sites. Both *P. latipinna* and *H. formosa*, two non-directed species, often required multiple drying events before successful re-colonization, apparently because they lack or have limited directed movement.

As expected, endurance tests revealed critical swimming speeds to be greater than ambient speeds estimated in nature using drift fences. However, the fastest species in our endurance tests were among the fastest in the field. For example, laboratory estimates revealed that *J. floridae*, *G. holbrooki*, and *F. chrysotus* were among the fast/high endurance species. Indirect estimates of speed derived from field data revealed that these three species were highly active and among the fastest of the five species (Obaza et al. 2011; Hoch et al. 2015; Bush 2017; Parkos III et al. 2019). Both field and laboratory data suggest that *J. floridae* and *G. holbrooki* are high endurance species that respond directionally to changing hydrology. Several studies have also described the rapid colonization potential of these two species (DeAngelis et al. 2005), and our models have demonstrated that their ability to rapidly colonize is directly related to physical endurance and directedness in movement. Additionally, our ABMs described species with low first-order arrival probabilities that were associated with slow, non-directed species. This was consistent with field data that described species with a life history associated with slow recovery following inundation (*H. formosa*, *P. latipinna)*.

Spatially structured population and community dynamics and dispersal have become a central theme in ecological studies and models (Bowler and Benton 2005). Understanding persistence of aquatic animals in wetlands, dryland rivers, and floodplains requires a dynamic spatial perspective

(Gibbs 1993; Junk and Wantzen 2004). Refuges from disturbance acting as sources of colonists increase regional population persistence and resilience (Poff and Ward 1990). Several studies have linked dispersal modes from source populations to recolonization success (Whitlatch et al. 1998; Negrello Filho et al. 2006). Our work has demonstrated individual behavioral and/or physiological characteristics underlie succession after disturbance with implications for resilience to disturbance on large spatial–temporal scales (Lancaster and Belyea 1997; Matthews 2012). Modeling such complex characteristics on both small and large spatial scales has proven difficult for ecologists and is hindered by a major gap in our empirical understanding of the mechanisms of colonization (Patterson et al. 2008).

Although random dispersal has been the predominant movement described in ecology, there has been increasing integration of directed, or non-random, dispersal into ecological theory (Yurk 2016; Row et al. 2017). Advances in movement ecology have been driven by improved analyses that rely on error-correction, calculation of movement, and statistical analyses designed for pattern recognition to classify individuals based on movement types. These statistical approaches require movement data derived from a variety of sources, such as satellite telemetry, to make inferences on movement patterns (Fauchald and Tveraa 2003; Austin et al. 2004; Patterson et al. 2008). Our models investigated movement by applying both field and laboratory estimates of speed and directedness to simulate movement, analyzing possible outcomes of recolonization, and relating model output to observed recolonization patterns. Our results indicate that coexisting species vary in the degree of directedness and speed, with predictable consequences for order of recolonization post disturbance. As important as directedness is for early recovery, species with little evidence for directed movement coexist in space and time with those that display it. Metacommunity models indicate trade-offs of dispersal ability and competitive ability may expected (Leibold and Chase 2017). Further exploration of community-wide variation in dispersal traits may be beneficial for understanding community assembly and persistence in environments facing increasing habitat fragmentation and environmental fluctuation.

ABM's have improved ecologist's ability to model movement in complex systems and explore the consequences of interactions among individuals and their environment (Grimm 1999; DeAngelis and Mooij 2005; Marceau 2008). We believe that the results from our ABM's are robust since we were able to compare results from our endurance tests and simulations to field estimates of speed and arrival order. Our ABM's provided an excellent medium to simulate colonization from refuge habitats and produced a simple model that proved effective in predicting dynamics of recolonization post-disturbance in a large ecosystem.

This study has demonstrated that colonization patterns can be predicted when a species' dispersal potential is quantified by estimating both speed and directedness. Also, we provide evidence that rapid colonization may not be correlated to population size. Our multi-method approach has improved our ability to understand post-successional dynamics and the mechanisms that drive biodiversity in spatially dynamic communities. However, these models focused solely on the behavioral and physiological aspects of colonization. Differences in other traits such as fecundity, somatic growth, and competitive ability may play a vital role in species coexistence post-colonization (DeAngelis et al. 2005). Further studies on post-colonization dynamics are needed to fully understand the drivers of species coexistence and biodiversity.

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Author contribution statement JVG helped design this study, conducted swim tunnel experiments, programed and carried out all data analyses and simulations, and wrote the manuscript. JCT helped design this study, solicited funding for and supervised collection of long-term field data, collaborated on data analyses and manuscript writing.

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