

Research Article

Cite this article: Charpentier JE, Gunn JS, Cheng MLH, Licht S, McCoy JH, Truscott JC, and Furey NB (2024). Invasive knotweed (*Polygonum* spp.) movement in a northern New Hampshire (USA) stream system. *Invasive Plant Sci. Manag.* doi: [10.1017/inp.2024.22](https://doi.org/10.1017/inp.2024.22)

Received: 19 December 2023

Revised: 2 May 2024

Accepted: 13 August 2024

Associate Editor:

Rob J. Richardson, North Carolina State University




Keywords:

Fallopia spp.; hydrochory; invasive species; movement ecology; riparian ecology; stream ecology

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Invasive knotweed (*Polygonum* spp.) movement in a northern New Hampshire (USA) stream system

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Abstract

Non-native plants negatively impact ecosystems via a variety of mechanisms, including in forested riparian areas. Japanese knotweed [*Polygonum cuspidatum* Siebold & Zucc.] and its hybrids (referred to as *Polygonum* spp. hereafter) are widely spread throughout North America and can impact flora and fauna of riparian habitats. Thus, information improving our ability to understand and predict the potential spread and colonization of *Polygonum* spp. is valuable. One dispersal mechanism is hydrochory (i.e., dispersal by water), including the downstream dispersal of viable stems that can facilitate rapid invasion within a watershed. We used passive integrated transponder (PIT) telemetry in experimental releases of *Polygonum* spp. stems to track the downstream transport of *Polygonum* spp. in a small (second-order) stream in northern New Hampshire, USA, in the summers of 2021 and 2022. A total of 180 (90 each year) *Polygonum* spp. stems were released at three sites within the stream reach, with 185 (~98%) being recaptured at least once, with a total of 686 recaptures. Individual relocated stems moved a maximum distance of 30 to 875 m downstream in 2021 and 13 to 1,233 m in 2022 during regular flows; however, a high-streamflow event in July 2021 flushed out all remaining stems downstream of the study area. Generalized additive mixed models (GAMMs) identified site-specific differences in stem movement rates and a general reduction in movement rates with increased duration of time elapsed since post-release. In general, *Polygonum* spp. stems moved farther downstream in sites with lower channel sinuosity, although other fine-scale habitat factors (e.g., water depth, habitat type, and presence of wood and debris jams) likely contribute to the ability for *Polygonum* spp. to further disperse or otherwise be retained within the channel. Thus, stream morphology and stream flow are likely to affect where *Polygonum* spp. stems will be retained and potentially reestablish. Predictive tools identifying areas of higher probability of hydrochory-based dispersal could help to focus removal efforts when employed or to identify riparian habitats at highest risk for spread.

Introduction

Non-native invasive plant species are a major cause of ecosystem degradation and impairment of ecosystem service benefits in the United States (Ferreira et al. 2021; Greene 2014; Lavoie 2017). Forested riparian areas provide many ecosystem service benefits to humans and are vital to the water quality of streams and rivers (Naiman et al. 1993; Riis et al. 2020). Riparian vegetation is adapted to natural flow regimes and supports high biodiversity and several essential ecosystem services for adjacent fluvial and terrestrial ecosystems (e.g., nutrient cycling, reducing leaching of pollutants, mitigating soil erosion, and producing soil organic matter; Su et al. 2022). However, riparian areas are at high risk of invasion by non-native plants because they are among the most human-disturbed ecosystems in the world (Allan and Flecker 1993; Greene 2014; Hammer and Gunn 2021; Lavoie 2017; Liendo et al. 2015).

Riparian ecosystems are structurally unstable due to frequent disturbances from water fluctuations (Naiman et al. 1993; Riis et al. 2020; Seeney et al. 2019; Wang et al. 2022); fluctuations in water levels outside the range of natural variability can trigger fundamental changes in composition and structure of riparian plant communities, which provides

Management Implications

Understanding dispersal distances and deposition patterns of *Polygonum* spp. (knotweed) is important for practitioners to implement site-specific restoration efforts on riparian vegetation, which can help facilitate effective control and removal efforts. We quantified the potential dispersal of *Polygonum* spp. stems in a second-order stream in New Hampshire, USA. Under generally low-to regular-flow conditions, *Polygonum* spp. dispersal was generally constrained to ~500 m of release, with initial dispersal distances linked to stream sinuosity (greater sinuosity resulted in greater retention) and time (most movements occurred soon after release). However, higher-flow events appeared to increase *Polygonum* spp. stem dispersal, and an extreme high-flow event in 2021 resulted in all stems being flushed downstream of our study system, implying that long-distance dispersal is possible via floods. Practitioners should also recognize that we only examined the potential dispersal of stems, while rhizomes generally contribute more to *Polygonum* spp. spread. Predictive tools identifying areas of higher probability of hydrochory-based dispersal by integrating stream habitats, flows, and *Polygonum* spp. biology could help to focus removal efforts or to identify riparian habitats that are at highest risk for spread within watersheds. Dispersal distances can be paired with mapping of *Polygonum* spp. along riparian habitats to identify reaches greatest at risk for invasion and at-risk habitats susceptible to erosion and degraded native plant diversity. For example, these data may be valuable for managers developing monitoring plans near *Polygonum* spp. stands after high-disturbance events such as logging. Early detection and rapid response efforts should be focused on reaches with higher sinuosity, complex habitats that can retain stems or rhizomes, and interventions immediately after higher flows recede.

opportunity for colonization by invasive non-native plant species (Richardson et al. 2007; Wang et al. 2022). Further, invasive plant species in northern latitudes frequently begin growth earlier in the spring than native species, reducing the resistance of native species (Wang et al. 2022). In conjunction with predictions of more frequent and severe flooding events in the northeastern United States, there is concern of significant potential for the development of a positive-feedback loop between increased non-native invasive species populations, more common and severe climate-induced flood events, erosion, and the dispersal of viable non-native invasive species propagules, especially *Polygonum* spp. (Houtt.) (Colleran and Goodall 2014).

Japanese knotweed [*Polygonum cuspidatum* (Houtt.) Ronse Decr.], also referred to as Itadori knotweed, is native to Asia and is one of the most invasive plants in the world. It is a rhizomatous perennial that grows rapidly in the spring and can form dense clonal patches (Rouleau et al. 2023). In its introduced range, *P. cuspidatum* is particularly abundant along riparian corridors (Colleran and Goodall 2014, 2015; Rouleau et al. 2023). In northern New England, USA, most *Polygonum* spp. plants are believed to be *P. cuspidatum*, although hybridization with giant knotweed [*Polygonum sachalinense* (F. Schmidt ex Maxim.) Ronse Decr.] produces the hybrid bohemian knotweed [*Polygonum xbohemicum* (J. Chrtek & Chrtková) Zika & Jacobson [*cuspidatum* × *sachalinense*]] (Gammon et al. 2007; Gammon and Kesseli 2010). In this study, we refer to all invasive knotweed plants as *Polygonum* spp. to allow for the possibility that

the study site contained any hybrid of *P. cuspidatum* and *P. bohemica* (Hammer and Gunn 2021). Invasive *Polygonum* spp. colonies are often associated with degraded forest structure and reduced stream habitat quality (Fogelman et al. 2018; Gerber et al. 2008; Lavoie 2017; Lecerf 2007; Seeney et al. 2019; Serniak et al. 2017; Urgenson 2006). The threat goes beyond a significant negative impact on plant biodiversity and forest structure. In particular, *Polygonum* spp. can have strong negative effects on instream macroinvertebrate decomposers, gastropods, amphibians, and native fish habitat (Colleran and Goodall 2015; Fogelman et al. 2018; Gerber et al. 2008; Lavoie 2017; Lecerf et al. 2007) and have also been found to reduce stream depths under low baseflow conditions (Vanderklein et al. 2014). *Polygonum* spp. is also associated with erosion (Kaehler 2023), likely by reducing ground cover (i.e., root structure of native plants) that holds soil in place during floods, which can inhibit the regeneration of native species that provide critical structural support to riverbanks (Colleran and Goodall 2015). Once established, *Polygonum* spp. is extremely difficult to eradicate and may have severe ecological, economic, or infrastructure effects (Colleran and Goodall 2015).

Although *Polygonum* spp. reproduces by seed, it spreads effectively through fragmentation once established, which most commonly takes place following flood events and mowing (Colleran and Goodall 2014, 2015). Across plants, hydrochory (i.e., dispersal by water) is the most prominent dispersal form in river systems, because many floating propagules are spread by water and deposit and establish on downstream riparian zones (Hyslop and Trowsdale 2012; Nilsson et al. 2010; Su et al. 2022). *Polygonum* spp. plant propagules (i.e., stem or rhizome fragments) are commonly washed downstream, because the brittle stems often extend over the stream and are easily broken off during high-flow storm events (Hammer 2019). Such transport can be the dominant vector of spread for this invasive plant along a river (Duquette et al. 2016), with areas closer to rivers associated with *Polygonum* spp. (Martin et al. 2019). Additionally, the poor ability of *Polygonum* spp. to stabilize banks can cause them to collapse into the stream, allowing individual plants, stems, or root and rhizome fragments to enter the stream channel (Arnold and Toran 2018; Hammer 2019; van Oorschot et al. 2017). Segments of stem or rhizome can sprout and successfully regenerate, even when the segment is exceptionally small, if the segment contains at least one node (Colleran and Goodall 2014; Rouleau et al. 2023). Yet spatial distribution of *Polygonum* spp. invasion along riparian corridors and factors that may determine distance of spread and likelihood of establishment are not well understood (Hammer and Gunn 2021; Wang et al. 2022).

Understanding potential dispersal distances and deposition patterns of *Polygonum* spp. stems is important for practitioners to implement site-specific restoration efforts on riparian vegetation. There is a need to discern how *Polygonum* spp. spreads so that effective proactive control and management measures can be prioritized and implemented. Identifying such factors can facilitate target control and removal efforts to minimize cost and maximize effectiveness. The purpose of our study was to quantify potential dispersal distances and deposition patterns of experimentally released *Polygonum* spp. stems and assess whether such metrics vary among stream reaches within a system with extensive *Polygonum* spp. patches. We used passive integrated transponder (PIT) tags combined with regular stream walks to assess downstream movements of *Polygonum* spp. stems. PIT tags are commonly used to assess movement of biota in stream systems (Bubb et al. 2008; Zydlewski et al. 2006) or even stream sediment

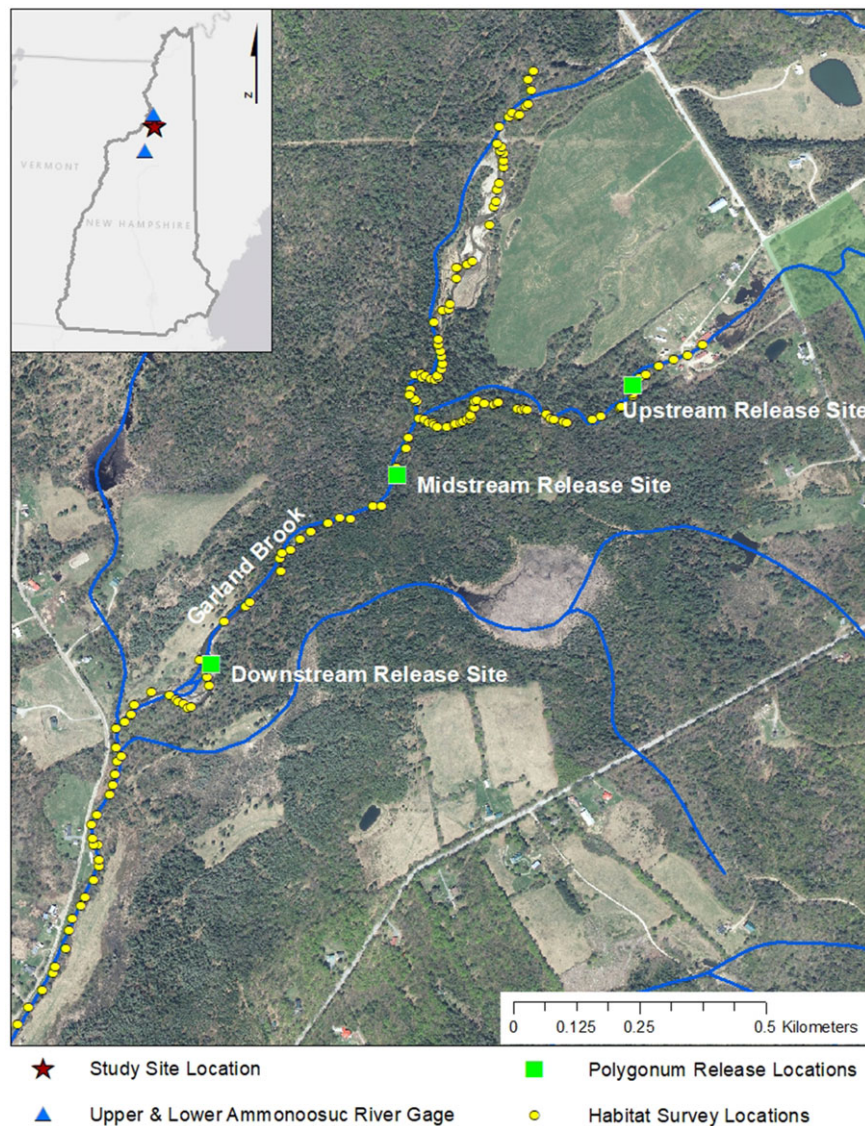


Figure 1. Study site location with upstream, midstream, and downstream *Polygonum* spp. release sites (green squares) along Garland Brook, Lancaster, NH, USA. Habitat survey locations (yellow circles) denote where individual habitat units were identified and measured (see Table 1).

transport (Arnaud et al. 2017; Lamarre et al. 2005), but for plants, PIT tags are generally only applied to seeds (Kempter et al. 2018; Suselbeek et al. 2013), and we are unaware of their use in quantifying potential hydrochory. Our study stream system, Garland Brook in northern New Hampshire, is a tributary to the Connecticut River, with its headwaters in the White Mountain National Forest. Garland Brook has well-known extensive *Polygonum* spp. patches (Hammer 2019). We hypothesized that: (1) total dispersal distances and movement rates of *Polygonum* spp. stems would vary among release sites, with higher stream sinuosity resulting in less *Polygonum* spp. movement; and (2) movement rates of *Polygonum* spp. stems would vary through time within the summer season.

Materials and Methods

Site Description

The headwaters of Garland Brook are in the Kilkenny Mountain Range in the White Mountain National Forest. Garland Brook is

located within Hydrologic Unit Code (HUC) 12-010801010804 (Jones et al. 2022; USGS 2023c). Several first-order headwater streams converge and flow in a single channel through an intact closed-canopy forest (Figure 1). The land surrounding Garland Brook is primarily agricultural with forested riparian buffers. Garland Brook contains a historic hydropowered logging mill (Garland Mill) that is heavily invaded by *Polygonum* spp. (Hammer 2019). *Polygonum* spp. is the dominant vegetation type on both sides of the mill access road, the mill property, and along the stream banks. The study site is located just downstream of the mill where Garland Brook begins to converge as it flows along both sides of a large pasture (Figure 1). Garland Brook continues through a matrix of forest, grazed pasture, and homesteads with an intermittent and narrow riparian buffer at the lower reaches before flowing into the Israel River (Hammer 2019; Figure 1). Stream surveys for terrestrial invasive plants conducted in the riparian areas along both sides of Garland Brook found 324 patches of invasive plants. *Polygonum* spp. is the most abundant invasive species in the study area (followed by Morrow's honeysuckle (*Lonicera morrowii* A. Gray) and glossy buckthorn (*Frangula alnus* Mill.) (Hammer 2019).

Table 1. Habitat assessment summaries for the 500 m downstream of each of the three release sites^a.

Release site	Sinuosity ^b	Mean gradient	Mean wetted width	Mean bankfull width	Mean depth at 50% width
		%		m	
Upstream	1.20	2.3 (±3.7)	5.5 (2.4)	6.5 (±2.6)	0.20 (±0.11)
Midstream	1.05	1.9 (±1.6)	8.6 (3.2)	10.3 (±3.1)	0.31 (±0.12)
Downstream	1.32	1.8 (±1.6)	8.2 (2.8)	12.3 (±3.2)	0.28 (±0.13)

^aValues shown for depth (m), wetted width (m), full width (m), and gradient (%), are mean values (±SD).

^bSinuosity = distance (stream)/500 m (straight-line distance).

Field Methods

Stream habitat was assessed before experimental releases in 2021. Starting at the downstream end of our study site (Figure 1), the primary habitat type was identified (i.e., pool, glide, riffle, or cascade) based on stream gradient and depth. Within each habitat unit, a series of measurements were collected, including gradient (percent), wetted width (m), bankfull width (m), length (m), and stream depth (m; taken at 25%, 50%, and 75% distances along the wetted width; Table 1). Stream depths and widths were taken at five latitudinal transects across the stream, at approximately equal distances along the habitat unit's length; these values were then averaged for each habitat unit and across habitat units within the section (Table 1). In addition, the dominant substrate type was noted, along with other metrics appropriate for fish habitat assessments being used in a separate study. The reach's thalweg (i.e., line of lowest elevation within streambed) was recorded via handheld GPS in each habitat unit. These thalweg locations were used to generate a line shapefile of the system. From these surveys and digitization of the thalweg, experimental release sites were identified (Figure 1; Table 1) based on their habitat characteristics and channel sinuosity. Channel sinuosity was quantified by measuring the total distance of the thalweg that falls within a straight-line distance of 500 m from the release site (calculated in ArcMap, ESRI, Redlands CA, USA). The upstream release site was described as a meandering, slow-moving channel; the midstream release site was a straight channel with many large in-stream boulders; and the downstream release site was a complex, braided, gravel-filled channel.

On June 14, 2021, and August 4, 2022, we conducted experimental releases of *Polygonum* spp. stems to assess downstream movements. Each *Polygonum* spp. stem was cut from the top 1 m of a stem from an established *Polygonum* spp. patch at each of the three release sites (upstream, midstream, downstream; see Figure 1). *Polygonum* spp. is well established throughout the study site. We used the top portion of *Polygonum* spp. stems in our experimental releases rather than rhizomes because (1) it was easier to maintain a similar size "unit" among released stems, (2) we assumed that the top portion of the plant was most likely to break off and enter the stream (we observed this anecdotally in the system in prior years), and (3) we could easily sample stems without digging out rhizomes and potentially causing erosion of stream banks in the field site. We recognize that although stems can sprout and lead to spread (De Waal 2001), rhizomes are likely the dominant mechanism of spread (Colleran and Goodall 2014; Gowton et al. 2016). Each released stem (approximately 1 m in length) had several nodes but no attached roots. We released *Polygonum* spp. stems with PIT tags. PIT tags (Biomark APT12, 12.5-mm long, 2.03-mm diameter, full duplex FDX-B; Biomark, Boise, ID) were glued to the stems and wrapped in electrical tape. Each stem was painted orange around the location of the PIT tag to increase the likelihood of detecting it after release during stream

walks. A total of 90 *Polygonum* spp. stems were released per field season ($n = 180$ between 2 yr), with 30 replicate stems released at each release site per field season. Stems were released at 30-s spacing intervals into the stream flow at river center. To relocate tagged stems, stream walks were conducted semi-regularly (described below), in addition to opportunistic searching during other related stream ecology studies in the system (unpublished data) in both field seasons. When tagged stems were found, their identities were recorded with a PIT tag reader (Biomark HPR Lite or HPR Plus). We also recorded any node shoots or sprouting, as this can occur rapidly (within weeks) from *Polygonum* spp. stems (De Waal 2001), and assessed whether any establishment occurred.

We assumed larger in-stream stem movements would happen in stages during higher flows; thus, we conducted stream walks to search for tagged stems after periods of elevated precipitation. We used the water gages for the nearby Ammonoosuc River to track rain events (<https://waterdata.usgs.gov>, site ID number 01130000 and 01137500; Figure 2) with follow-up monitoring within 5 d of large rain events (defined as $> \sim 12.7$ to 25.4 mm of rain). There were also final monitoring visits at the end of each of the 2021 and 2022 field seasons to record ending locations of stems, if established, and to collect the stems released in the study.

Data Analysis

PIT tag detections and their associated latitudes and longitudes were brought into a geographic information system (GIS) using ArcMap v. 10.8.2 (ESRI). Garland Brook's thalweg was digitized (Figure 3) from in-stream habitat assessments (Figure 1; Table 1) and aerial imagery (Figure 1). Habitat unit characteristics were considered among habitats within 500 m downstream of each release site (Table 1). The location of each tagged *Polygonum* spp. stem recapture was assigned a stream position (meters from release to the nearest location of the thalweg) using the Locate Features Along Routes tool in ArcMap (Figure 3). Any obvious false detections (i.e., detection upstream of the release site) were removed. Any small (<5-m) upstream "movements" of PIT tags were presumed to be GPS measurement error and were treated as no movement (given the same location as previous detection).

Kruskal-Wallis tests were used to determine whether the maximum downstream distance moved by *Polygonum* spp. stems varied among the three released sites in each year. When these tests were significant, pairwise Wilcoxon tests with continuity correction were used to identify which release sites significantly differed in maximum downstream distance moved. To further analyze how downstream movements varied with time and among the three release sites in both years, we used a generalized additive mixed model (GAMM) framework. Movement rate (m d^{-1} between successive recaptures of individual *Polygonum* spp. stems) was the response variable, with the release site (upstream, midstream, or downstream) and duration of time since release (in decimal days) as candidate explanatory variables. The smoothed term (duration

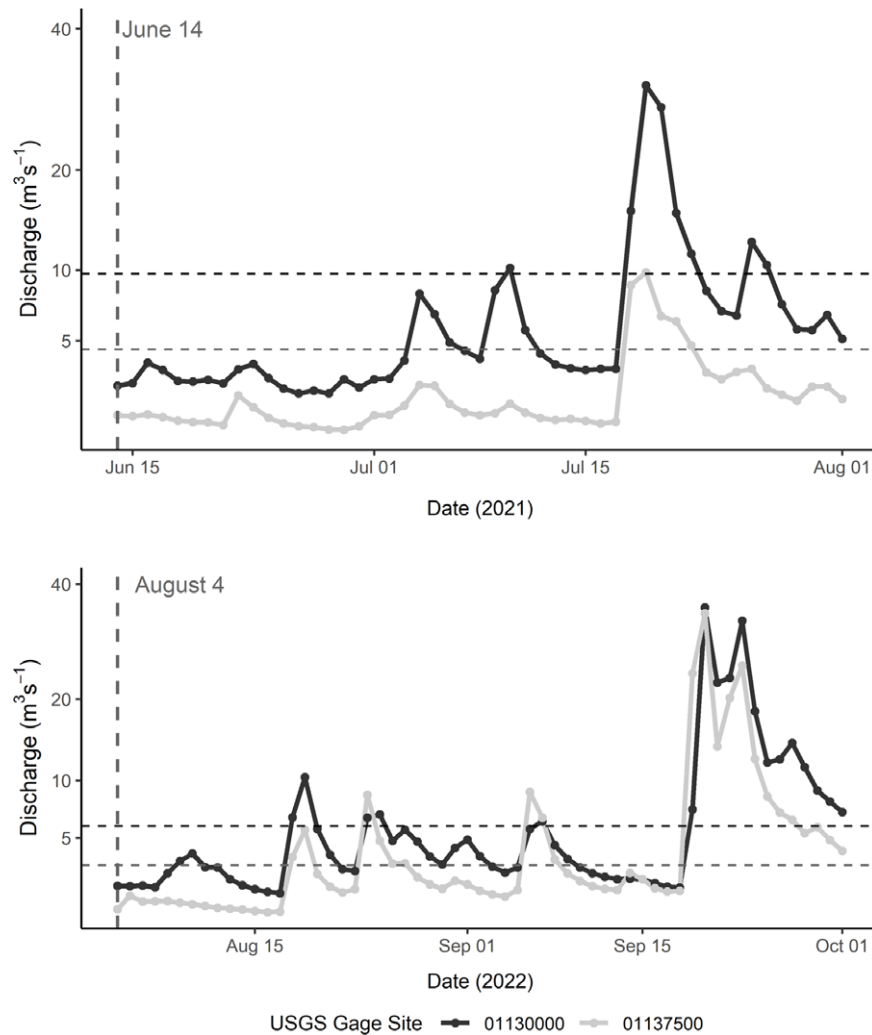


Figure 2. Upper and Lower Ammonoosuc River gages (Upper = north of Garland Brook: gage site 01130000; USGS 2023b; Lower = south of Garland Brook: gage site 01137500; USGS 2023a) for 2021 and 2022 field seasons (source: <https://waterdata.usgs.gov>). Vertical dashed lines represent release date of experimental *Polygonum* spp. stems, with date labeled top left. Horizontal dashed lines represent mean discharge values for each USGS gage site for the dates shown between 1991 and 2023. Note the seasonal difference in dates along the x axis between the two panels.

of time since release) was fit using a penalized thin-plate regression spline (Wood 2003). Separate models were constructed for each release year. Due to the repeated captures of some *Polygonum* spp. stems, we included the *Polygonum* spp. identity as a random effect in all models. To reduce potential for overfitting to the continuous variable of time since release, we limited the number of effective degrees of freedom to three ($k=4$). We used the Akaike information criterion (AIC) to rank models containing both or one of the two explanatory variables, with lower AIC values indicating more parsimonious models. We used the MGCV package (Wood 2011, 2017) in R v. 4.2.2 (R Core Team 2022) to construct GAMMs.

Results and Discussion

Polygonum spp. Stem Recaptures

In 2021, the 90 released stems of *Polygonum* spp. were recaptured 369 times, and in 2022 the 90 released *Polygonum* spp. stems were recaptured 317 times. Of the 90 released stems in 2021, 87 stems (~97%) were detected at least once (maximum 7 times); 88 (~98%)

of 90 stems released in 2022 were detected (maximum 6 times). Maximum distances moved from individual release sites varied between 30 m and 875 m downstream in 2021 (mean = 155 m; SD = 142 m) and 13 to 1,233 m in 2022 (mean = 283 m, SD = 220 m; Figure 4). In both years, the maximum distances tracked of *Polygonum* spp. stems differed significantly among the three release sites (2021 Kruskal-Wallis test $P < 0.0001$; 2022 Kruskal-Wallis test $P < 0.0001$). In 2021, the mean maximum distance moved was highest for stems released at the upstream site (208 m, SD = 49 m), intermediate for the midstream site (161 m, SD = 175 m), and lowest for stems released at the downstream site (97 m, SD = 150 m; Figure 5). Pairwise Wilcoxon rank-sum tests indicated the maximum distances moved differed significantly among all pairs (downstream–midstream $P = 0.017$; downstream–upstream $P < 0.0001$; midstream–upstream $P = 0.0002$), even though the median maximum distances moved were quite similar between segments released downstream (76 m) and midstream (73 m). In 2022, significant differences were detected in the maximum downstream movements among the three release sites (Kruskal-Wallis test $P < 0.0001$), with stems released at the midstream site (468 m) traveling farther than those released upstream (240 m) or

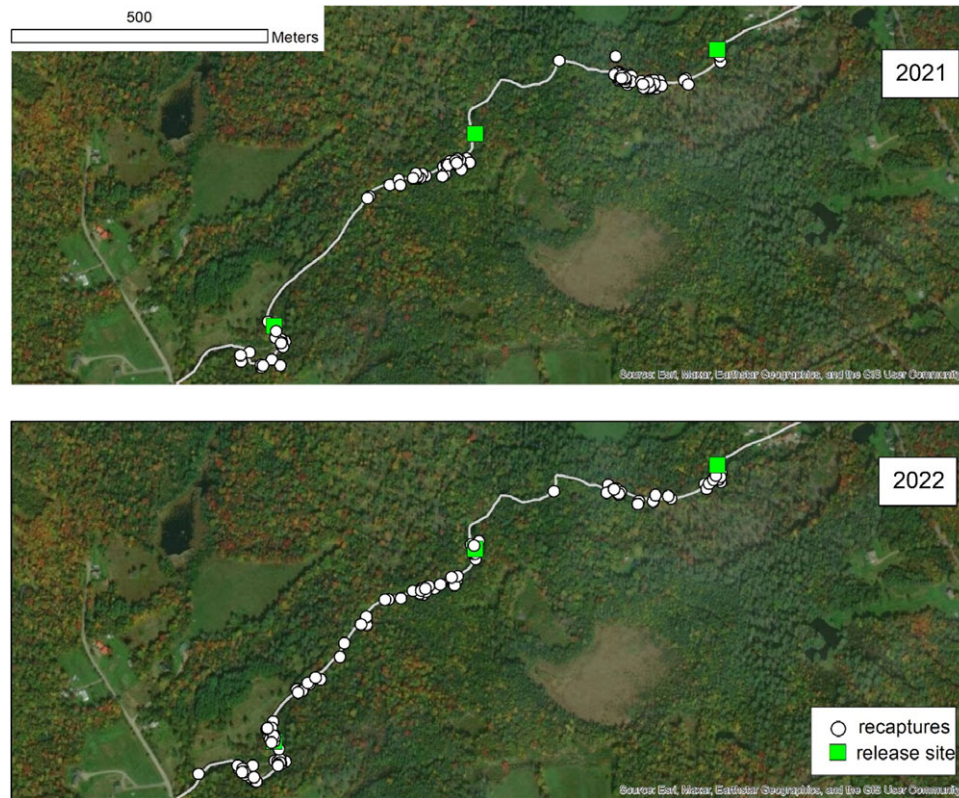


Figure 3. *Polygonum* spp. movement for 2021 and 2022 field seasons. Recapture events (white circles) are all via passive integrated transponder (PIT) tag detection; each *Polygonum* spp. stem could be detected multiple times.

downstream (132 m). Similarly in 2022, stems released downstream experienced the least maximum downstream dispersal (mean = 132 m, SD = 62 m), but midstream-released stems experienced the highest downstream dispersal (mean = 468 m, SD = 203 m), and upstream-released stems dispersed an intermediate distance (mean = 240 m, SD = 202 m; Figure 5). All pairwise comparisons in the maximum dispersal distance among the three release sites were significantly different for each year (Wilcoxon rank-sum test for all 2021 pairwise comparisons $P < 0.05$; in 2022, all $P < 0.0001$). Thus, maximum distances moved varied among release sites, consistent with our original hypothesis.

Polygonum spp. Stem Movement Rates

GAMMs examining variability in movement rates of *Polygonum* spp. stems identified both time since release and release site as important explanatory variables. For both years' models, these two variables were retained in models with the lowest AIC values (Table 2). Time since release appeared to be the more important explanatory variable; the second-best model for both years retained this variable rather than release site and had higher percent deviance explained, following our original hypothesis and expectations (stems will travel upon release until they become entangled or beached, then movements will slow or stop until the stem is freed again). In 2021, stem movement rates experienced a nonlinear relationship with time since release; fastest movement rates occurred shortly after release, which then declined slowly over the first week post-release (Figure 6). Movement rates increased in mid-July 2021, coinciding with periods of increased in-stream flow. In 2022, this relationship was largely monotonic,

with fastest movement rates experienced shortly after release and then declining in a near-linear fashion as the time since release increased. Coefficients for release sites (Table 3) indicated that movement rates were slower for downstream sites in both years (Figure 6); this was presumably driven by the lack of faster movements (no stems released downstream were ever observed moving $> 50 \text{ m d}^{-1}$) rather than a clearly lower median or mean value. In parallel with our maximum-distance investigations, movement rates were more variable between midstream and upstream sections between the 2 yr. *Polygonum* spp. stems in the downstream release site consistently dispersed less than the *Polygonum* spp. stems in the midstream or upstream release sites (Figure 5). These results are consistent with our original hypothesis that movements of *Polygonum* spp. stem would be site dependent within the stream.

Hydrochory of *Polygonum* spp. and Influences of Stream Characteristics

In general, *Polygonum* spp. stems across sites were recaptured within 500 m of their original release sites under generally low flows in 2021 and low to regular flows in 2022, with all recapture events occurring within 2 km of release locations, consistent with previous studies, where downstream dispersal distances of mimic propagules were limited to 3 km from release (Su et al. 2022) and rapidly decreasing probability of recapturing released plant fragments with distance below point of release (Didier et al. 2023; Riis and Sand-Jensen 2006). Generally, *Polygonum* spp. patches along rivers are found in near proximity, even if the spread was not specifically monitored (e.g., $< 100 \text{ m}$ between patches; Hart et al. 1997). Thus, retention of *Polygonum* spp. stems was generally

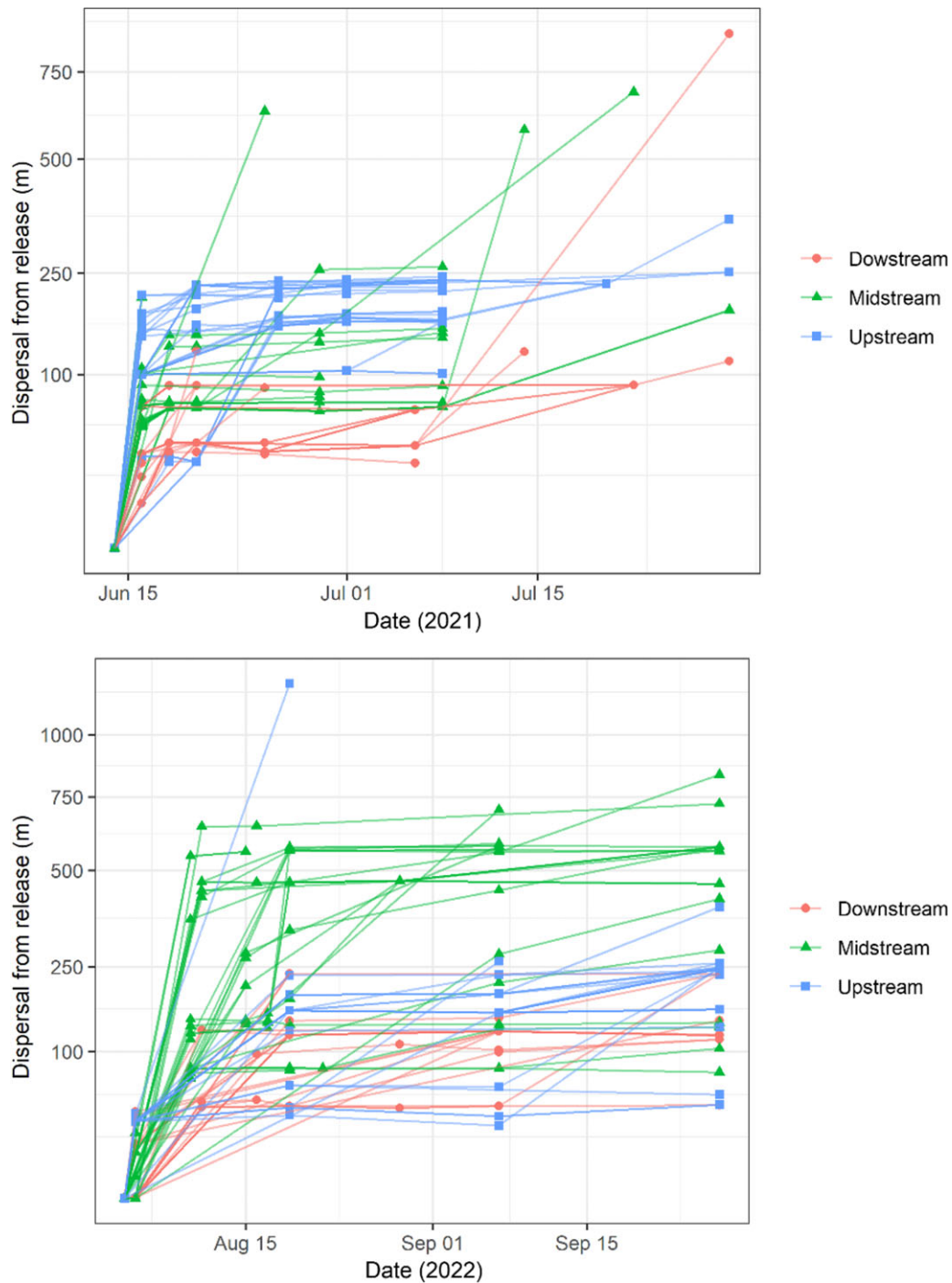


Figure 4. Downstream dispersal distance through time of *Polygonum* spp. stems in 2021 (top) and 2022 (bottom).

high at these flows, with the greatest potential for hydrochory to be impactful at the reach scale rather than among stream orders. Most new *Polygonum* spp. plants originate from rhizome fragments, with only ~15% to 30% originating from stems (Colleran and Goodall 2014; Gowton et al. 2016); however, this is a higher rate of success than individual seeds (3%; Gowton et al. 2016) and the combination of rhizomes and stems can be the dominant vector for spread in riverine systems (Duquette et al. 2016). At the start of the growing season, *Polygonum* spp. dedicates more energy toward stem growth than rhizomes (Colleran and Goodall 2015),

highlighting that stem regrowth and establishment are likely still important contributors to dispersal.

Although not consistently significant across all analyses, there was evidence that *Polygonum* spp. stems released in the downstream habitat, characterized by higher sinuosity, traveled shorter distances and less quickly. Stream sinuosity is generally considered to promote retention of coarse organic matter (James and Henderson 2005), although broad-shaped or leaf-life matter is more easily retained than dowel- or rod-like shapes (James and Henderson 2005), and sinuosity is not always predictive of

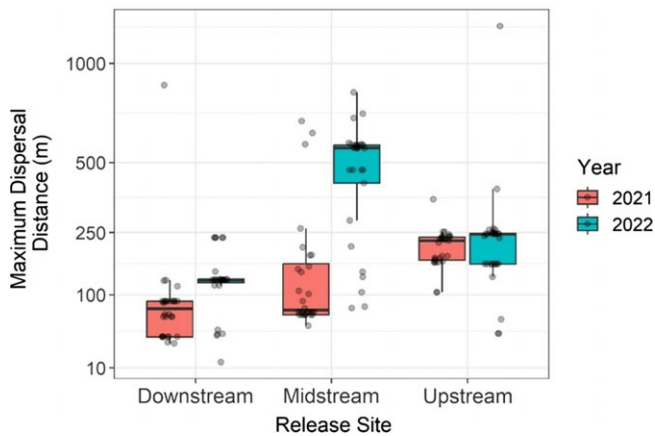


Figure 5. Maximum dispersal distance of *Polygonum* spp. stems for each year and release site.

dispersal distances in hydrochory (Su et al. 2022). Regardless, bank curvature has been positively correlated with presence of *Polygonum* spp. deposited on stream banks (Didier et al. 2023), supporting the role of stream sinuosity in deposition of *Polygonum* spp. In addition to stream sinuosity, we observed potential differences in in-stream habitat that may have also contributed to decreased movements in stems released at the downstream site. Although not directly measured or characterized, the downstream site in particular had several overturned logs or other dense stems of vegetation within the bankfull width, resulting in opportunities for *Polygonum* spp. to be retained via snags at a given location for days to weeks. Such snags are more likely to retain coarse matter than boulders (James and Henderson 2005) that were observed more in the midstream reach. Increased contact among the streambed, stream bank, and vegetation (whether it be native or non-native) should increase retention of stems (Riis and Sand-Jensen 2006). Thus, identifying and quantifying potential areas where *Polygonum* spp. stems are likely to make contact may improve predictive frameworks for identifying habitats likely to retain *Polygonum* spp. dispersed via hydrochory. Nonetheless, many of these traits (presence of in-stream vegetation, large woody debris, or complex habitat and in-stream vegetation) that we associated with *Polygonum* spp. stem retention can be associated with more tortuous or sinuous streams, relative to straight channels (Diez et al. 2001; Nakamura and Swanson 1994).

Beyond stream geomorphology, flow conditions and regimes can affect hydrochory, with deposition more likely to occur on receding flow regimes (Hyslop and Trowsdale 2012; Merritt and Wohl 2002; Su et al. 2022; van Leeuwen et al. 2014). Although not specifically compared, in general, *Polygonum* spp. dispersed more in 2022, when flows were generally higher than in 2021 (with the exception of the flood event described below) and with more above-average flow events during our specific field season (Figure 2). Flows in 2021 were generally low, with *Polygonum* spp. dispersing generally only <250 m, but a very high-flow event in mid-July 2021 resulted in multiple stems being dislodged and further dispersed, followed by the eventual loss of all stems from the study area under extreme flows. Thus, our estimates of high retention and relatively low dispersal distances (within ~500 m) of *Polygonum* spp. stems are specific to normal or low flows; with higher flows and floods likely resulting in greater potential dispersal, as observed with increased dispersal in generally higher flows in 2022 and the flood event in 2021 that flushed stems even farther, downstream of our study area. In summary, stream hydrology and

fluvial geomorphology, along with the biology (Hyslop and Trowsdale 2012) of *Polygonum* spp., will likely dictate the success of hydrochory in allowing *Polygonum* spp. to establish downstream.

Considerations for *Polygonum* spp. Reestablishment

For hydrochory to be successful, the stem or propagule would need to be deposited successfully in suitable habitat and growth conditions, while the stem is still viable. *Polygonum* spp. stem viability does not extend past the second spring following its dispersal (Colleran and Goodall 2015). Our work at Garland Brook supports this time frame, as stems recaptured in the 2022 field season from 2021 releases appeared to be dead and were not established into the riverbanks or riparian ecosystem; they were simply retained on or within the woody debris along the riverbank. Within a given study season, the majority of released *Polygonum* spp. stems developed node shoots, consistent with rapid bud and node shoot development ($\sim 2.9 \text{ mm d}^{-1}$) within weeks (De Waal 2001), but we never observed establishment at the end of each field season. Generally, fragments or seeds of plants are deposited along shallow slopes (Su et al. 2022) or areas associated with still water (pools or eddies; Hyslop and Trowsdale 2012). Unvegetated shallow slopes along the riparian zone are likely to be ideal for seed or fragment deposition as well as regrowth or establishment (Su et al. 2022) via increased light that can promote growth of shoots (Martin 2019). Given we largely described dispersal of stems during normal flows, most stems we monitored were deposited within the banks of the channel, on snags and large woody debris. Deposition within the banks of the channel, versus higher up on banks, might not represent ideal habitat for reestablishment. Our study only quantifies potential dispersal patterns via hydrochory. Broadly, *Polygonum* spp. is most successful in disturbed habitats (Navratil et al. 2021; but see Didier et al. 2023) with high light availability (Dommanget et al. 2013). More specifically, if the propagules deposit in the riparian zone as water levels recede (likely aided by floods or increased flows), they could have a higher chance to colonize due to ideal growing conditions (e.g., moist soil), and long-term submergence of habitat could reduce aboveground native vegetation (Su et al. 2022), providing further opportunities for successful invasion.

Study Limitations

Our ability to describe the potential dispersal of *Polygonum* spp. is dependent on our ability to track individually marked stems. PIT telemetry is robust in that tags do not have batteries and are durable over time. However, their read range (the maximum distance between receiver and the tag that still allows for detection) is generally quite short ($\sim 0.3 \text{ m}$), requiring us to individually locate and scan tags. In addition, tag collisions are possible when many tags are co-located; such aggregations occurred at retention “hotspots” such as log jams and snags where at times >10 tags were located at a single habitat unit for several days. We took efforts to slowly scan through the group and repeating this process over days likely minimized chances of missing tags completely. Our approach also required us to be able to identify and see stems to scan with hand units; future research that installed PIT arrays across the stream could more comprehensively quantify when individual stems reached certain distances downstream. Finally, we could not locate how far and how quickly any stems moved once they were downstream of our study reach (e.g., after the 2021 high-flow event). Regardless, we had high rates of detection of marked

Table 2. Generalized additive mixed model (GAMM) results for modeling *Polygonum* spp. stepwise movement rates (m d⁻¹ between successive recaptures).

Model rank ^a	Model	AIC	ΔAIC	% Deviance explained
2021				
1	Release site + time since release + (random: tag ID)	3,081.0	0	38.8%
2	Time since release + (random: tag ID)	3,130.0	49	32.6%
3	Release site + (random: tag ID)	3,244.6	163.6	3.07%
4	(random: tag ID)	3,252.1	171.1	<0.01%
2022				
1	Release site + time since release + (random: tag ID)	2,853.3	0	17.5%
2	Time since release + (random: tag ID)	2,868.8	15.5	12.3%
3	Release site + (random: tag ID)	2,889.6	36.3	5.82%
4	(random: tag ID)	2,904.6	51.3	<0.01%

^aModels are ranked by Akaike information criterion (AIC).

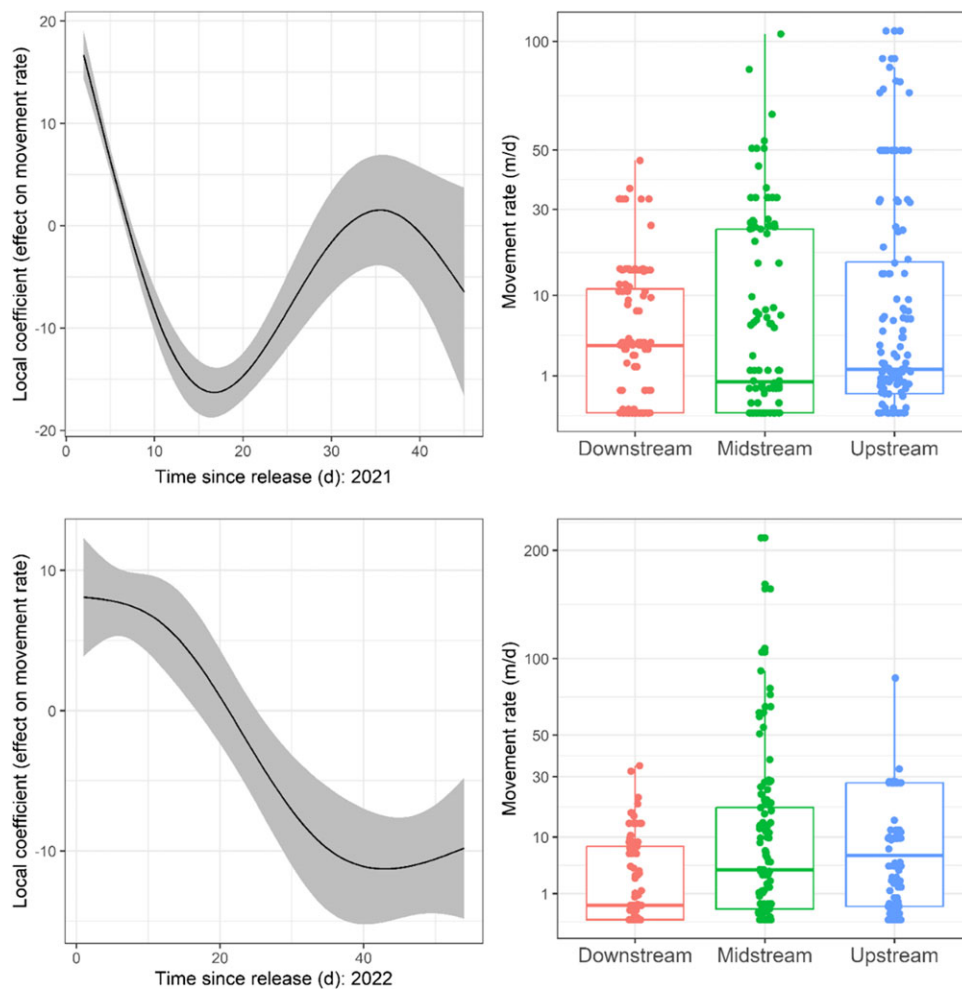


Figure 6. Left, Generalized additive mixed model (GAMM) model fits showing smoothers between days since release and movement rates for 2021 (top) and 2022 (bottom). Right, Movement rates (m d⁻¹ between successive relocations) between years and among release sites.

stems and thus are confident we adequately described their general dispersal distances.

Conservation and Management Implications

The ability of *Polygonum* spp. to disperse via water for hundreds of meters even under regular flows likely contributes to the ability to quickly invade and impact stream and riparian habitats.

Identifying characteristics that contribute to *Polygonum* spp. propagules being released could help further build predictive frameworks for *Polygonum* spp. spread in stream ecosystems across settings (across flow variations, natural spread vs. after high-disturbance events such as logging, etc.). The root system of *Polygonum* spp. promotes erosion along stream banks (Arnold and Toran 2018; Colleran et al. 2020; Kaehler 2023; Matte et al. 2022), which in turn can promote propagule dispersal, especially during

Table 3. Model coefficients for the top-ranked models (from Table 2) explaining variability in *Polygonum* spp. stem stepwise movement rates (m d⁻¹ between successive recaptures) for each year^a.

2021	Parameter	Estimate	SE
Parametric	Intercept (downstream)	3.97	2.79
	Release site (midstream)	6.39	3.12
	Release site (upstream)	14.98	7.51
Smooth	Parameter	edf	
	Time since release	2.99	
2022	Parameter	Estimate	SE
Parametric	Intercept (downstream)	4.02	2.24
	Release site (midstream)	13.79	3.05
	Release site (upstream)	8.20	3.04
Smooth	Parameter	edf	
	Time since release	2.75	

^aEach generalized additive mixed model (GAMM) can include both parametric variables (release site) and continuous factors evaluated by a smoothing function ("Smooth"; time since release). For the smoothed variable, the effective number of degrees of freedom (edf) used by the smooth is stated.

high flows (Colleran et al. 2020), generating a potential reinforcing feedback loop via continued erosion and dispersal. In response, studies have suggested focusing control efforts on *Polygonum* spp. patches most susceptible to erosion and thus propagule dispersal (Colleran and Goodall 2014, 2015).

Complications in managing *Polygonum* spp. arise from its plasticity in environmental tolerance, resilience to disturbance, vegetative dispersal capabilities, and extensive energy storage in rhizomes (Gillies et al. 2016; Hocking et al. 2023). Numerous control methods have been studied (e.g., covering, cutting, burning, digging, and encapsulation) and herbicidal control is considered the most effective (Hocking et al. 2023), but all methods are expensive (Rouleau et al. 2023). However, the use of herbicides to control invasive species should be done with caution, as the use of chemicals has its own set of environmental consequences, especially in and around riparian areas. Continuing to improve frameworks for predicting dispersal and establishment dynamics of *Polygonum* spp. in riparian areas will help prioritize control efforts.

In conclusion, we provide estimates of dispersal potential in a small New England stream, with *Polygonum* spp. stems generally dispersing <500 m from release sites under low and regular flows, with higher flows increasing dispersal distance and extreme flow events having the capacity to push stems presumably several kilometers. These short-term dispersal distances are weakly correlated with stream characteristics, including sinuosity and presence of large woody debris or snags; although in-stream large woody debris may not be ideal for *Polygonum* spp. establishment, stream reaches with increased sinuosity may experience greater retention of *Polygonum* spp. stems and increased chances of spread. In addition to sinuosity, short-term dispersal distances were also negatively correlated with time since release, with only times of increased flow resulting in further movements shortly after release. Such information on stream channel morphology, habitats, and flow variation can be paired with mapping of *Polygonum* spp. along riparian habitats to identify reaches that are at greatest risk for invasion for potential early detection; subsequent impacts of *Polygonum* spp., such as erosion (Arnold and Toran 2018; Colleran et al. 2020; Kaehler 2023; Matte et al. 2022); and negative impacts to local plants and diversity (Colleran and Goodall 2015; Wilson et al. 2017).

Acknowledgments. We appreciate regional landowners who allowed us to access field sites via their properties. Additional field efforts were provided by N. Hermann and C. Pearson. C. Hammer's MS thesis (University of New Hampshire) helped inspire this work.

Funding statement. This research was supported by the Dick George Fund provided to the Natural Resources and Environment Department at the University of New Hampshire. Furey was partially supported by the Class of 1937 Professorship in Marine Biology from the University of New Hampshire's School of Marine Science and Ocean Engineering.

Competing interests. The authors declare no conflicts of interest.

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