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Research Article

Functional trait interactions drive seed buoyancy and dispersal strategies in *Echinocystis lobata*

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Abstract

Hydrochory (water dispersal) is a major driver of plant invasions in riparian landscapes but both the diaspore traits that determine flotation and the contribution of water-mediated transport to the colonization success of non-native species remain insufficiently understood. *Echinocystis lobata*, an alien vine widely naturalized along European rivers, provides a suitable model for testing how seed morphology governs buoyancy and, consequently, hydrochorous dispersal potential. The main aim of this study was to examine how functional traits influence the buoyancy of *E. lobata* seeds, which can be classified as normal seeds, freely released from fruits, and trapped seeds, retained within fruits.

We investigated three hypotheses under controlled laboratory conditions: (H1) seed mass, particularly in interaction with thickness, determines sinking probability; (H2) surface area affects flotation mainly through interactions with mass; and (H3) trapped seeds differ functionally from normally released seeds. Using a generalized linear mixed-effects model, we demonstrated that buoyancy is governed by non-linear interactions among mass, thickness, and surface area, with distinct patterns for trapped versus normal seeds. Thin normal seeds floated longer as mass increased, whereas in trapped seeds higher mass accelerated sinking. Surface area influenced flotation only when combined with mass and trapping status. Normal seeds remained buoyant for up to 14 days, while trapped seeds sank sooner (≤11 days).

These findings highlight that variability in diaspore traits generates a broad spectrum of dispersal outcomes, supporting both local deposition and long-distance hydrochoric transport. Understanding how trait-vector interactions shape dispersal enhances invasion risk prediction and informs management strategies, such as removing reproductive plants near waterways before fruit maturation. Overall, our results demonstrate that hydrochory, amplified by diaspore heteromorphism, may be a key driver increasing the invasiveness of *E. lobata* in European river valleys.

Key words: Hydrochory, invasive alien plants, nautohydrochory, riparian ecosystems, seed dimorphism

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Introduction

Understanding how water-mediated dispersal shapes the spread of non-native plants provides essential insight into the mechanisms facilitating rapid range spread of many herbaceous non-native species (Boedeltje et al. 2004; van den Broek et al. 2005; Jansson et al. 2005; Carthey et al. 2016). Invasive alien plants are particularly successful because they often combine multiple dispersal strategies that jointly enhance their colonization capacity (Sádlo et al. 2018). Human activities further reinforce these processes by promoting long-distance transport across geographic and climatic barriers, thereby increasing ecological success (Richardson et al. 2000). Such interactions between natural dispersal modes and anthropogenic influences create a powerful synergy that accelerates invasion dynamics (O'Loughlin et al. 2017). While the initial release of diaspores from parent plants initiates propagule flow, subsequent redistribution by secondary vectors strongly influences invasion outcomes (Vander Wall et al. 2005; Schupp et al. 2010; Kowarik and Säumel 2008). Secondary dispersal determines whether diaspores remain close to the maternal plant or reach distant sites, thereby altering colonization probability, gene flow, and the ability to occupy new environments (Vander Wall et al. 2005; Schupp et al. 2010).

In riparian systems, secondary dispersal is especially important because seeds shed on land may later be transported by water to entirely new locations (Jansson et al. 2005). Once deposited, they can establish populations far away from their source (Andersson and Nilsson 2002). These secondary movements significantly extend dispersal distances, facilitate escape from predators and pathogens, and promote establishment in heterogeneous habitats (Hämäläinen et al. 2017). As a result, they are central to both persistence and spread of alien plant species (Vander Wall et al. 2005). Hydrochory, particularly dispersal by floating on the surface of water, represents one of the most effective secondary pathways operating in rivers and floodplains (Sádlo et al. 2018; Boedeltje et al. 2004; Parolin 2005). Through this mechanism, riparian corridors act not only as habitats but offer routes of rapid spread (Gurnell et al. 2008; Anđelković et al. 2022). Propagules transported downstream are frequently deposited on geomorphic features such as bars, benches, and floodplains (van den Broek et al. 2005). These habitats, characterized by recurrent disturbance and high resource availability, provide ideal conditions for germination and seedling establishment (Jansson et al. 2005). At the same time, seasonal floods redistribute diaspores over wide areas, maintaining dynamic seed banks and enabling repeated colonization events (Andersson and Nilsson 2002).

Hydrochory encompasses a range of dispersal processes. Not only light diaspores, but also heavier fruits or vegetative fragments, can be carried by water, depending on their morphology and local hydrodynamic conditions (Boedeltje et al. 2004). Traits such as seed mass, shape, surface area, and the presence of air-filled tissues strongly determine buoyancy and retention time in water. For example, samaras of *Ailanthus altissima* display clear adaptations enhancing flotation and dispersal efficiency (Boedeltje et al. 2004; Carthey et al. 2016). In urban rivers, such samaras are effectively transported downstream, contributing to the spread of exotic trees such as *Acer negundo* and *Ailanthus altissima* (Kowarik and Säumel 2007; Säumel and Kowarik 2013). Other studies emphasize that seed-coat structures such as air cavities, thickened walls, or fibrous surfaces can modulate buoyancy and prolong hydrochoric dispersal in invasive species (Carthey et al. 2016; Najberek et al. 2020). Seeds with fibrous surfaces or specialized cavities may remain afloat for extended periods, increasing the probability of reaching suitable deposition sites (Carthey et al. 2016; Najberek et al. 2020). Small modifications of seed coat morphology can substantially prolong flotation and enhance dispersal success (Boedeltje et al. 2004). Nautohydrochorous dispersal of seeds is strongly influenced by fruits' morphology, with structural traits such as shape, internal cavity (or hollow chamber), and dehiscence mechanisms determining whether seeds are transported individually by water or released explosively, thereby affecting dispersal distance and spatial distribution (Niwa 2024). However, despite these insights, the interplay between seed morphology and dispersal potential remains insufficiently understood. This is particularly true for species that produce dimorphic diaspores. Studies on hydrochory have shown that in *Cyclachaena xanthiifolia*, an invasive North American species with heterocarpy, smaller, lighter, and moderately flattened seeds with a small surface area sink after about 12 h, whereas larger, heavier, strongly flattened seeds with a wide rim and greater surface area float for up to 24 h, confirming the influence of seed shape and surface area on buoyancy (Lhotská and Slavík 1969). In such plants, different propagules may vary in mass, shape, or protective structures, which in turn influences their likelihood of being transported and successfully establishing (Carthey et al. 2016).

A striking example of a riparian invader illustrating these processes is the North American vine *Echinocystis lobata*. This fast-growing annual climber has spread rapidly across Europe and Asia, where it has colonized numerous river valleys (Klotz 2009). Genetic analyses reveal that European populations are structured, reflecting multiple introductions and regional differentiation (Jocienė et al. 2023). Such genetic variation may interact with environmental context to shape dispersal performance. For instance, fruits produced by plants growing in more natural, less disturbed habitats tend to be larger, heavier, and contain more seeds than those produced in disturbed areas (Kostrakiewicz-Gierałt et al. 2022). These differences in fruit morphology translate into variation in buoyancy, flotation duration, and ultimately dispersal distance. As a consequence, even within the same species, propagule dispersal potential is not fixed but context-dependent, reflecting both genetic background and environmental influences (Boedeltje et al. 2004; van den Broek et al. 2005).

Dispersal in *E. lobata* has traditionally been attributed to barochory and blastochory, with seeds dropping from drying capsules or being released explosively from dehiscent fruits (Silvertown 1985; Najberek et al. 2020). However, a significant proportion of diaspores remain enclosed within fibrous fruits, which delay release and facilitate secondary transport by wind or water (Dylewski et al. 2018). Approximately one third of fruits contain trapped seeds that are less accessible to rodents and may persist longer in riparian habitats. These fruits, buoyant due to their fibrous structure, can float downstream before releasing seeds (Dylewski et al. 2018). Hydrochory therefore appears central to the invasion success of *E. lobata*, as both buoyancy and flotation duration directly determine colonization potential (Kowarik and Säumel 2007; Fryirs and Carthey 2022). In this way, rivers and valleys act as key corridors for the spread of *E. lobata* in Europe, linking distant populations and facilitating continuous range spread (Zając et al. 2011).

The coexistence of normal and trapped seeds reflects a diversified dispersal strategy. Substantial variation in seed morphology, including size, mass, and shape, likely affects flotation potential and transport distance (Carthey et al. 2016). Nevertheless, how functional differences between propagule types influence the dispersal potential of *E. lobata* in riverine landscapes remains poorly known. These knowledge gaps are critical for understanding *E. lobata* invasion ecology. Moreover, mechanistic insights into seed buoyancy can enhance invasion risk predictions and guide targeted control (Zając et al. 2011). By identifying vulnerable stretches of rivers and clarifying the role of different seed traits in dispersal, management actions can be made more spatially coordinated and cost-effective (Patinet et al. 2023).

This study examines how seed traits shape dispersal performance in *E. lobata*. We focus on the ways in which morphological features such as mass, thickness, surface area, and shape interact to determine buoyancy. We ask whether seeds retained within fibrous capsules differ functionally from freely released seeds in their flotation potential, and how fruit morphology regulates the timing of seed release into aquatic systems. By analyzing these relationships, we aim to clarify the mechanisms by which hydrochory contributes to invasion success in this species. We hypothesized that: **H1** - seed mass would strongly influence sinking probability, particularly through its interaction with thickness; **H2** - surface area would affect flotation mainly in combination with other traits and exert only a limited independent effect; **H3** - trapped seeds would differ functionally from normal seeds, with buoyancy shaped by unique interactions among mass, thickness, and surface area. These hypotheses were tested in controlled laboratory conditions during which we examined the buoyancy of normal and trapped seeds after measuring their functional traits: mass, thickness, and surface area.

Material and methods

Study species

Echinocystis lobata (Michx.) Torr. & Gray., commonly known as wild cucumber or balsam apple, belongs to the *Cucurbitaceae* family. It is a monotypic genus, the name derived from Greek echinos (hedgehog) and kystis (bladder), referring to its spiny fruits. The species originates from North America, where it is widespread in the eastern United States, except for California and parts of the southeast, and southern Canada, mainly in Ontario and Quebec (Choate 1940; Stocking 1955; Alex 1998; Gerrath et al. 2008; Callahan and Lincoln 2022). It occurs in moist habitats such as riverbanks, wetlands, forest edges, and anthropogenic sites. It had been also introduced to some parts of the western United States (Callahan and Lincoln 2022).

Invasion history

E. lobata was introduced to Europe in the late 19th and early 20th centuries as an ornamental plant and soon escaped cultivation (Domin 1942; Heine and Tschopp 1953; Slavík and Lhotská 1967; Dajdok and Kącki 2003; Zając et al. 2011). It spread rapidly across central and eastern Europe, extending from Central Europe to the Russian Pacific coast (Probatova 1987). In many countries, it is now recognized as a troublesome invasive species (Tokarska-Guzik 2005; Klotz 2009). In Poland, first wild populations were noted in the early 20th century, likely introduced from both Germany and Ukraine (Tokarska-Guzik 2005). By the mid-1960s it had established in the Carpathians, and by the 1990s its range expanded rapidly, colonizing riparian zones across the country (Zając et al. 2011; Zając and Zając 2019). Today, it is widespread in moist habitats, particularly river valleys, and often forms dense, monospecific stands (Maćkowiak and Dylewski 2014).

Morphology and reproduction

The plant is a vigorous annual vine, climbing with branched tendrils (Fig. 1). Its fruits are inflated, spiny capsules containing 1 to 6 seeds, most commonly four (Slavík and Lhotská 1967). Fruits usually have two or three chambers (locules),

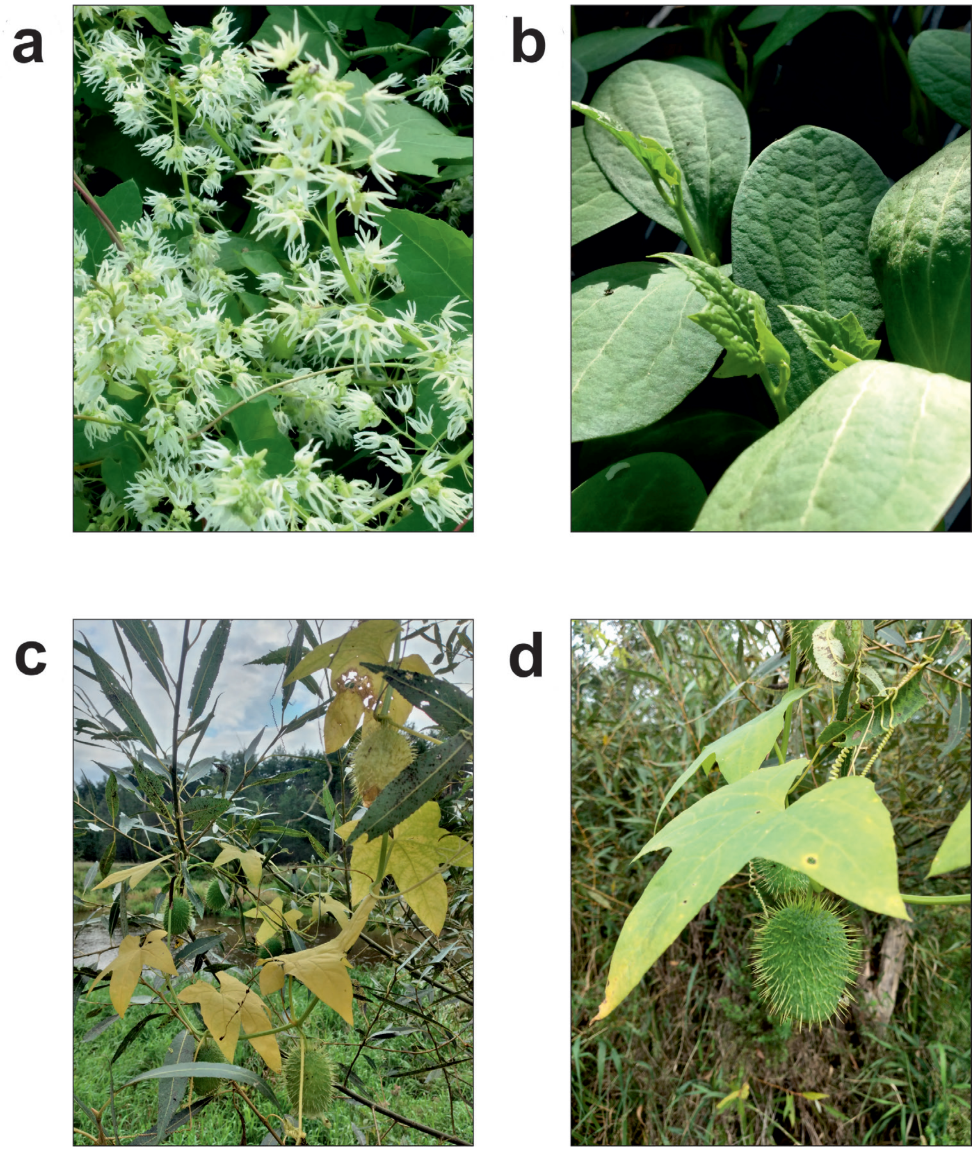

Figure 1. Reproductive and vegetative structures of *Echinocystis lobata*. **a.** Inflorescences; **b.** Seedlings; **c.** Plants climbing the willows along the Liwiec River; **d.** Ripening fruit.

although occasionally a single-chambered fruit develops at the tops of the shoots toward the end of the growing season. (Fig. 2). As fruits dry, the distal part of the pericarp ruptures, releasing seeds. However, fibrous internal structures often retain seeds, delaying their release (Silvertown 1985; Dylewski et al. 2018).

A unique trait of *E. lobata* is the production of additional trapped seeds within the fibrous framework of the fruit. On average, 34% of fruits contain such seeds, which remain protected from predation and may be released only after decomposition of the capsule (Dylewski et al. 2018). Trapped seeds differ slightly in weight and shape from normally released seeds but show similar germination potential. Their delayed dispersal enhances persistence in riparian habitats (Silvertown 1985; Dylewski et al. 2018). Recent observations indicate that stem anatomy and climbing behavior of *E. lobata* vary with support availability; shoots grow fastest and display pronounced nutation when suitable supports are dense, and their hollow pith with reinforcing sclerenchyma and collenchyma tissues facilitates efficient climbing (Dołkin-Lewko and Zajączkowska 2024).

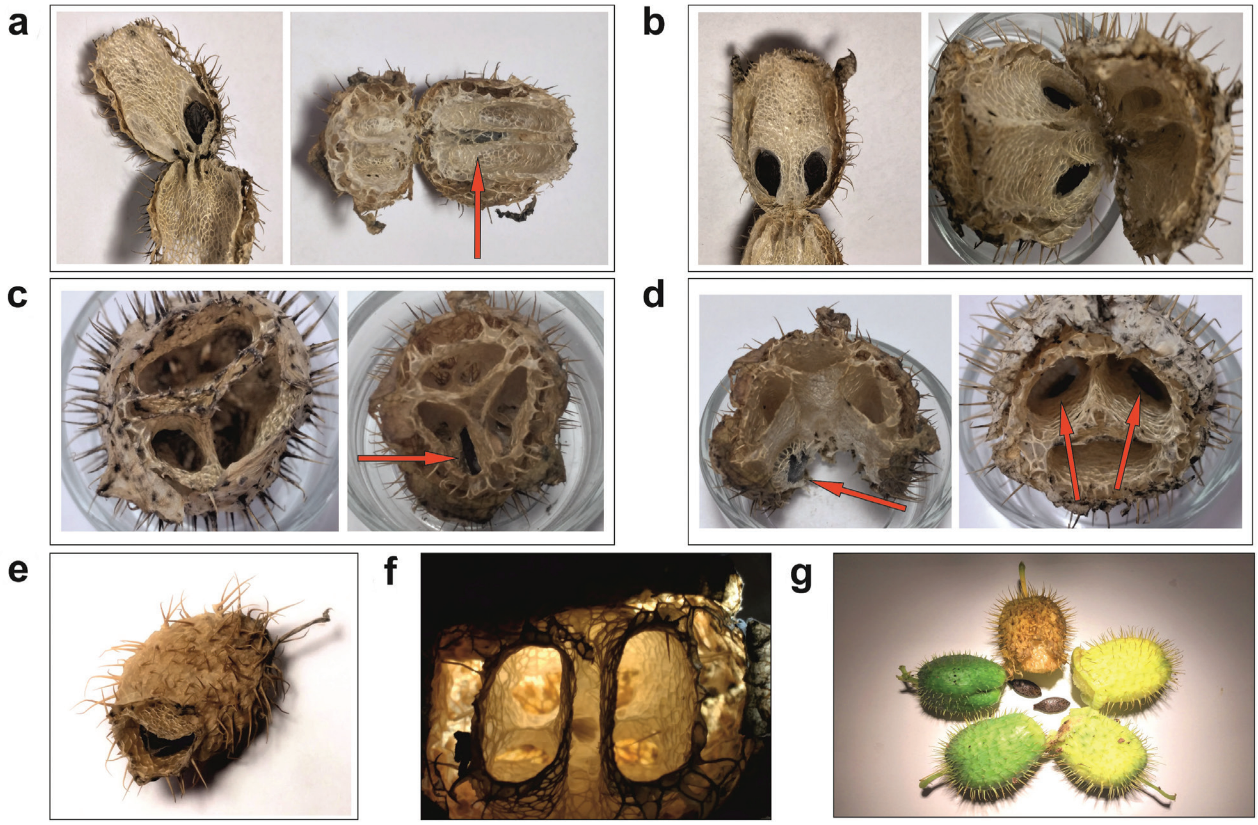

Figure 2. Fruit diversity in *Echinocystis lobata*. **a.** Two-loculus fruit with one trapped seed; **b.** Two-loculus fruit with two trapped seeds; **c.** Three-loculus fruits, with one trapped seed (right); **d.** Three-loculus fruits, with one trapped seed (left) and two trapped seeds (right); **e.** One-loculus fruit; **f.** The interior of a normal fruit with two loculus (most common type); **g.** Fruits in various stages of ripeness. Red arrows indicate barely visible trapped seeds.

Location of seed collection points

Six populations of *E. lobata* distributed in Poland in the Bug and Liwiec river valleys were selected for the study (Fig. 3). Four sites are located in the Bug valley, three of which are in the Lower Bug Valley mesoregion (Skuszew [52°35.85'N, 21°29.78'E], Szumin [52°36.36'N, 21°37.22'E], Wywłoka [52°37.02'N, 21°40.63'E]) and one in the Podlasie Bug River Gorge mesoregion (Drażniew [52°22.43'N, 22°42.56'E]) (Kondracki 2002). Two sites are located in the Liwiec valley. The Liwiec River is a left-bank tributary of the Bug, and *E. lobata* sites are situated near its mouth (Koszelanka [52°33.94'N, 21°35.96'E]) and (Barchów [52°30.73'N, 21°38.54'E]). These sites are located in the transition zone between the Lower Bug Valley and the Wołomin Plain mesoregions. All sites occur within the zone of regular spring flooding and occasional summer floods caused by heavy rainfall.

Seed measurement methods

Mature fruits were collected between October and December 2024. After harvest, fruits were classified into two categories: (i) fruits with normal seeds, i.e., seeds freely released after capsule dehiscence, and (ii) fruits with trapped seeds, i.e., seeds retained by fibrous structures inside the capsule and not released during natural drying. At each site, 100 fruits containing trapped seeds were collected first. An equal number of fruits with normal seeds was then gathered so that the

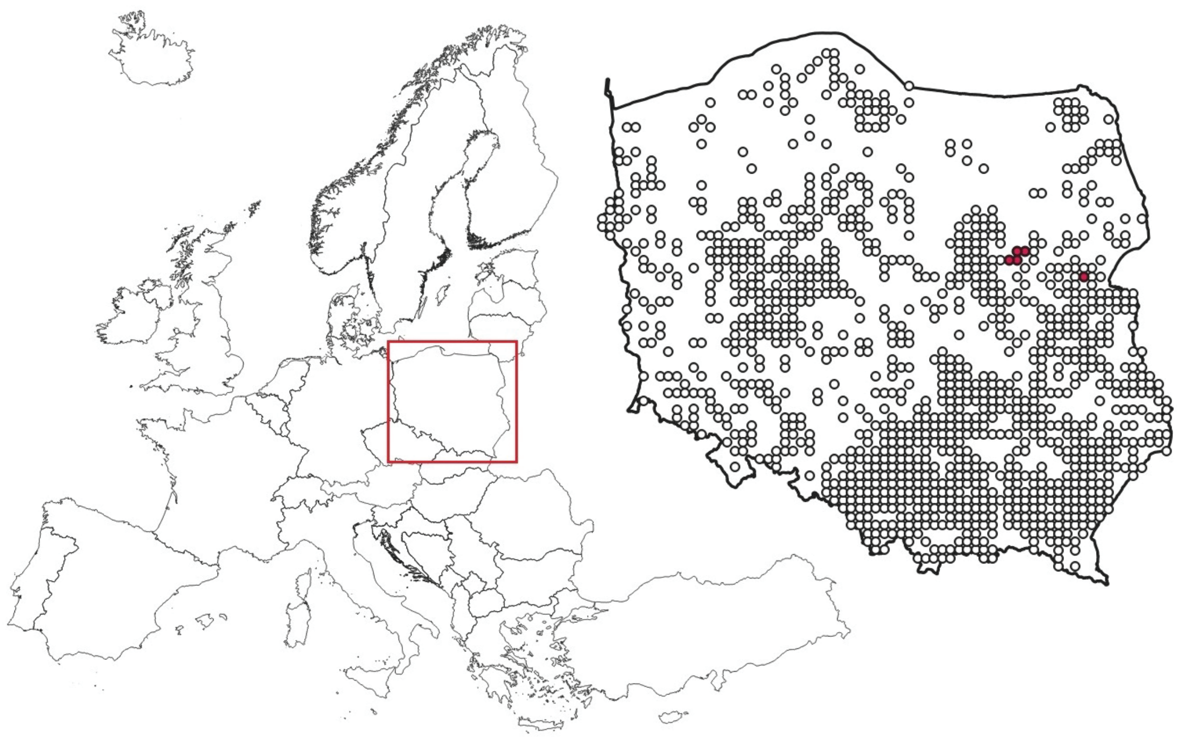

Figure 3. Location of the studied *Echinocystis lobata* sites (red points) against the background of the species distribution map in Poland (white points) in the ATPOL grid (Zając and Zając 2019).

quantities of trapped and normal seeds from each site were the same. In total, 681 normal seeds and 681 trapped seeds were tested across six populations. Abnormally developed seeds (immature or malformed) were excluded from the analyses. Preliminary experiments conducted in 2023 demonstrated that both trapped seeds and seeds remaining afloat on the water surface were capable of germination.

Trapped seeds were identified by shining a flashlight into the fruit chamber, which made the retained seeds visible through the capsule walls. They were then manually extracted using a scalpel. Each seed was weighed, labeled with an individual number, placed in a separate envelope, and stored in sealed plastic containers. Storage took place under ambient outdoor conditions for approximately three to four months, i.e., from harvest until the buoyancy experiment.

We measured the following seed traits: length, width, thickness (mm), and fresh weight (g). Measurements were made using an electronic caliper and a laboratory scale. Seed surface area (mm^2) was calculated using the ellipse formula (πab), where a and b are half the length and width, respectively. Additionally, we calculated the shape coefficient (width/length), where values <0.5 indicated elongated, lanceolate to oval seeds, and values >0.5 indicated oval to nearly spherical seeds.

Buoyancy experiment

The buoyancy experiment was conducted outdoors between February and March 2025, coinciding with the period of natural river flooding due to ice floes or snowmelt. Temperatures during the experiment ranged from 1 to 7°C, preventing ice formation in the containers. Seeds were placed individually into transparent plastic containers (100 ml) filled with unfiltered river water. River water was used to account for its natural ionic composition and organic matter, which may influence flotation. Prior to the experiment, the water was stored under the same conditions as the seeds. To avoid confusion, seeds were introduced one by one. The number of floating seeds was recorded every 24 hours over a 14-day period. To simulate natural turbulence, containers were gently shaken once per day during monitoring.

Statistical methods

We conducted all statistical analyses using R 4.3.1 (R Core Team 2025). To evaluate how seed traits shape s in shaping the probability of sinking, we fitted a generalized linear mixed-effect model with binomial error distribution. The model included five interaction terms among five predictors. Specifically, we examined (i) the effect of seed mass on seed area, (ii) the interaction between thickness and mass, and (iii) the influence of seed type (normal vs. trapped) on area, thickness, and mass. Model diagnostics based on a non-parametric dispersion test indicated no signs of under- or overdispersion (dispersion parameter = 0.995, P = 0.976).

Study site was included as a random factor to account for population-level variation. We calculated marginal (Rm^2) and conditional (Rc^2) coefficients of determination, reflecting variance explained by fixed effects alone and by both fixed and random effects, respectively. The difference (Rc^2 - Rm^2) indicates the proportion of variance attributable to population identity.

In interpreting the model results, we placed greater emphasis on effect sizes than on P values. This decision reflects growing concern that P-values are highly sensitive to sample size: large samples may yield statistically significant results for negligible effect sizes, while small samples may fail to detect effects that are biologically meaningful (Wasserstein and Lazar 2016). Therefore, model predictions were visualized as marginal responses, i.e. predicted values while holding other predictors constant.

To evaluate our model describing the probability of seed sinking, we compared it with a corresponding intercept-only (null) generalized linear mixed-effect model using the corrected Akaike Information Criterion (AICc). A lower AICc value for the full model relative to the null model indicated that inclusion of the explanatory predictors provided a better supported description of the data.

Results

Trapped seeds were generally smaller and lighter than normal ones (Table 1), sank faster, and remained afloat for a shorter time (Fig. 4). Our results show that seed morphology and trapping status jointly affect buoyancy and sinking probability in *Echinocystis lobata* (Fig. 5).

Table 1. Functional traits of trapped and normal seeds: length, width, thickness and mass.

Location	n	Trapped seeds				Normal seeds			
		Length [mm]	Width [mm]	Thickness [mm]	Mass [g]	Length [mm]	Width [mm]	Thickness [mm]	Mass [g]
Barchów	119	15.89	8.20	3.97	0.27	17.57	8.73	3.97	0.32
Drażniew	117	16.15	8.43	3.75	0.27	17.82	8.80	3.80	0.33
Koszelanka	107	16.27	8.35	4.18	0.29	17.95	8.47	4.10	0.32
Skuszew	117	16.26	8.32	4.26	0.30	18.46	8.78	3.92	0.34
Szumin	111	15.97	8.78	3.74	0.27	17.35	8.56	3.72	0.30
Wywłoka	110	16.41	8.56	4.02	0.29	18.44	8.94	3.90	0.32
mean		**16.16**	**8.44**	**3.99**	**0.28**	**17.93**	**8.71**	**3.90**	**0.32**

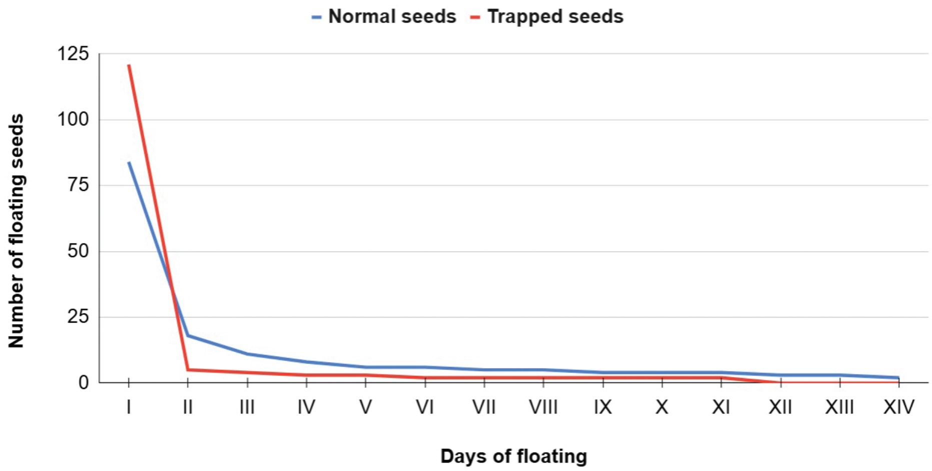

Figure 4. Percentage and buoyancy time of floating seeds divided into normal and trapped seeds.

Functional traits and buoyancy of normal and trapped seeds

We characterized the functional traits of normal and trapped seeds (Table 1). Trapped seeds were generally smaller than normal ones, particularly in length (mean 1.77 mm) and width (mean 0.27 mm). The two seed types also differed in mass due to their size differences. Trapped seeds had a lower mean mass (0.04 g) compared to normal seeds. They also had a slightly greater mean thickness (0.09 mm), although this difference was minimal. The shape coefficient (width/length) differed slightly between seed types. Normal seeds had a mean coefficient of 0.49, indicating more elongated to oval shapes, whereas trapped seeds had a higher mean value of 0.53, corresponding to more oval to nearly spherical forms.

The proportion of floating normal seeds was 12.3% and trapped amounted to 17.8%. After the first day, 2.6% of normal seeds and 0.7% of trapped seeds floated. After 48 hours, the proportion of floating normal seeds dropped to 1.6%, and trapped seeds to 0.6%. Trapped seeds sank faster (up to 11 days), while normal seeds remained up to 14 days (Fig. 4).

Predictors and interactive effects of seed traits on sinking probability

A generalized linear mixed model revealed that seed mass, thickness, and their interactions with trapping status significantly influenced sinking probability (Table 2), explaining 43% of its variance, while the random effect of study site contributed only modestly (11%).

An effect of seed size on the probability of sinking was markedly influenced by seed mass (Fig. 5a–c). For seeds with a lower mass (≤ 0.25 g), the probability of sinking increased from 9% at a size of 0.38 cm^2 to 45% at 0.77 cm^2 (Fig. 5a). For medium-weight seeds (0.26 < seed mass ≤ 0.35 g), it increased from 3% at a size of 0.38 cm^2 to 27% at 0.77 cm^2 (Fig. 5b), while for heavier seeds (> 0.35 g) it increased from 1% at a size of 0.38 cm^2 to 16% at 0.77 cm^2 (Fig. 5c). The relationship between seed mass and the probability of sinking was subtly influenced by seed thickness (Fig. 5d, e). For thin seeds (≤ 0.30 cm), the probability of sinking decreased from 75% at a mass of 0.12 g to 5% at 0.52 g (Fig. 5d). For thicker seeds (> 0.30 cm), it decreased from 52% at a mass of 0.12 g to 0% at 0.52 g (Fig. 5e).

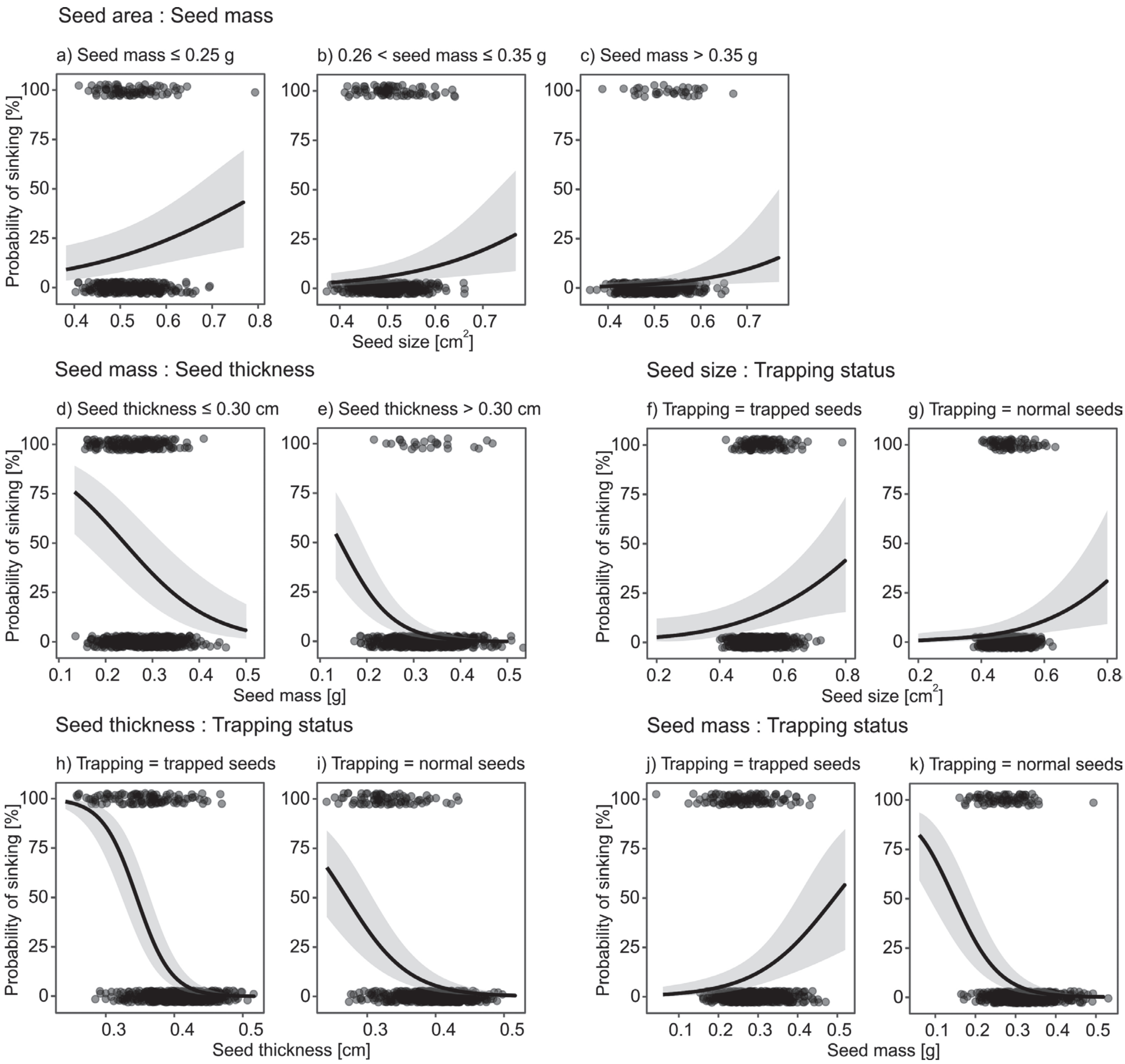

Figure 5. Predicted relationships between *Echinocystis lobata* seed sinking probability and key morphological traits based on the generalized linear mixed-effect model (Table 2). **a-c.** Effect of seed area on sinking probability across three seed-mass classes: light (≤0.25 g), medium (0.26-0.35 g), and heavy (>0.35 g). **d, e.** Interaction between seed mass and thickness: thin seeds (≤0.30 cm) versus thick seeds (>0.30 cm). **f, g.** Seed surface area influences sinking in trapped versus normal seeds. **h, i.** Effect of seed thickness depending on trapping status. **j, k.** Seed mass interacts with trapping status to determine sinking. Black lines represent model predictions, grey bands indicate 95% confidence intervals, and points show observed values.

The relationship between seed size and the probability of sinking was only slightly affected by trapping status (Fig. 5f, g): in trapped seeds, the probability of sinking increased from 3% at 0.20 cm^2 to 42% at 0.80 cm^2 (Fig. 5f), while in normal seeds it increased from 1% at 0.20 cm^2 to 31% at 0.80 cm^2 (Fig. 5g). We observed a similarly gentle effect of trapping status on the relationship between seed thickness and sinking probability (Fig. 5h, i). For trapped seeds, the probability of sinking decreased from 98% at 0.24 cm thickness to 0% at 0.51 cm (Fig. 5h), whereas for normal seeds, it decreased from 65% at 0.24 cm thickness to 0% at 0.51 cm (Fig. 5i). The relationship between the probability of seed sinking

Table 2. A generalized mixed-effect linear model of *Echinocystis lobata* seeds sinking probability depending on seed traits and trapping status (AICc = 791.8; $AICc_0$ = 1052.1). RE - SD of random effects. Parameters of the generalized linear mixed model (GLMM) describing the probability of seeds sinking as a function of seed traits and trapping status (AICc = 791.8; $AICc_0$ = 1052.1). RE - standard deviation of the random effect (study site). The table presents coefficient estimates, standard errors (SE), z-values, significance levels, and the variance of the random effects.

Predictor	Estimate	SE	Z	Pr(>|z|)	RE SD	R^2_m	R^2_c
(Intercept)	2.581	0.689	3.744	<0.001	0.882	0.429	0.538
Seed mass: seed size	21.764	7.676	2.835	0.004			
Seed mass: seed thickness	-7.255	0.937	-7.742	<0.001			
Seed size: trapping status = trapped seeds	-1.072	2.398	-0.447	0.654			
Seed thickness: trapping status = trapped seeds	-1.794	0.434	-4.127	<0.001			
Seed mass: trapping status = trapped seeds	27.801	3.543	7.846	<0.001			

and their mass was strongly affected by the trapping status (Fig. 5j, k). For trapped seeds, it increased from 1% at a mass of 0.06 g to 57% at 0.52 g (Fig. 5j), while for normal seeds, it decreased from 82% at a mass of 0.06 g to 0% at 0.52 g (Fig. 5k).

Discussion

Our study demonstrates that buoyancy of *Echinocystis lobata* seeds is shaped by complex, non-linear interactions among morphological traits, particularly mass, thickness, surface area, and shape. Importantly, these relationships differed between normal and trapped seeds, indicating functional divergence between seed types. Overall, our results confirm that hydrochory represents an effective mechanism of dispersal in this invasive climber, with seeds maintaining buoyancy long enough to facilitate downstream transport (Fryirs and Carthey 2022).

Comparable mechanisms have been reported elsewhere. Guja et al. (2010) showed that many coastal diaspores maintain buoyancy in saline water for weeks, and germination often resumes once seeds are returned to freshwater. Similarly, Fumanal et al. (2007) linked heteromorphism in *Ambrosia artemisiifolia* seeds to diversification of dispersal potential and recruitment niches, a pattern mirrored by the dimorphism observed in *E. lobata*. Observations from flooded forests also suggest that seed mass and density respond to hydrological conditions: diaspores of different species from inundated habitats often have lower specific mass and increased air-filled tissues, improving buoyancy (Lopez 2001). Kowarik and Säumel (2007) found that 81% of *Ailanthus altissima* samaras could drift on rivers for up to 20 days while retaining germination capacity, indicating that floating propagules may persist and establish far downstream.

H1. Influence of seed mass and thickness on buoyancy

Our first hypothesis (H1) predicted that seed mass strongly determines sinking probability, particularly in interaction with thickness. This prediction is supported by our results, which show that the effect of seed mass on buoyancy depends on seed thickness (Fig. 5d, e). Surprisingly, in thin seeds, higher mass enhanced flotation, likely by stabilizing orientation on the water surface, whereas thick seeds sank regardless of mass, highlighting the importance of morphological context in determining sinking probability. This observation corresponds to findings from Najberek et al. (2020), who demonstrated that structural adaptations in the seed coat, such as thicker external layers and air cavities, can offset mass-related sinking in *Impatiens glandulifera*, enabling even relatively heavy seeds to remain afloat. These results deviate from the expectation that greater seed mass accelerates sinking by increasing density. Carthey et al. (2016) showed that seeds with higher density sink more rapidly, as greater mass relative to volume reduces their buoyant potential and floating time in fluvial systems. Instead, they highlight the importance of morphological context: thin seeds may exploit surface tension more efficiently when heavier, while thick seeds sink regardless of mass due to reduced surface-to-volume ratio. Comparable interactive effects have been reported for other riparian taxa: Boedeltje et al. (2004) showed that even heavy diaspores can disperse long distances by water, depending on buoyancy traits, while Vander Wall et al. (2005) stressed that secondary dispersal mechanisms may overcome physical constraints.

In *E. lobata*, such variation in mass and thickness creates a spectrum of dispersal potentials from seeds restricted to local deposition to those drifting for days. This diversity likely enhances colonization success across heterogeneous riparian habitats. Our findings are consistent with research demonstrating that morphological and genetic variability within *E. lobata* populations may underpin differences in dispersal performance. Kostrakiewicz-Gierałt et al. (2022) reported that fruit size, seed number, and seed mass varied systematically with habitat conditions and vertical fruit position, implying that hydrochory potential may differ among stands. Jocienė et al. (2023) further showed that European populations display clear Amplified Fragment Length Polymorphism-based genetic structuring, most likely reflecting several introduction sources; such differentiation could interact with local selection on dispersal traits. In addition, studies on seed removal indicate that seed size and toughness influence predation intensity by rodents (Dylewski et al. 2018), potentially altering the window of opportunity for hydrochoric transport. Together, these data highlight that both phenotypic plasticity and evolutionary divergence may contribute to the broad range of dispersal capacities observed in *E. lobata*.

H2. Role of seed surface area in flotation

Our second hypothesis (H2) predicted that surface area would exert only limited independent effects but would interact with other traits, such as trapping status.

The observed interaction between these two traits confirms H2 (Fig. 5a–c, f, g), which is important because this interaction affects seed buoyancy and therefore the dispersal potential of *E. lobata* via hydrochory, influencing colonization success and invasion dynamics. In trapped seeds, larger surface area increased sinking probability, whereas in normal seeds the effect was weak. This suggests that water interacts differently with seed coats depending on seed type: larger trapped seeds may absorb water faster, increasing density and accelerating sinking, while normal seeds remain less affected. Moreover, the thickness-trapping interaction reinforces this pattern: thin trapped seeds sank rapidly, whereas thicker seeds resisted sinking regardless of trapping status (Fig. 5h, i). These findings align with earlier studies showing context-dependence of surface-related traits. Carthey et al. (2016) demonstrated that small, irregularly shaped diaspores may exploit surface tension to prolong flotation, while Chambert and James (2009) noted that larger propagules can travel farther under favorable conditions. Najberek et al. (2020) similarly observed that in *Impatiens glandulifera*, surface-related features such as seed coat texture and the presence of air-retaining structures modulated buoyancy, often in interaction with seed mass and thickness. The patterns highlighted by Jansson et al. (2005), where flooding increased the number and diversity of colonizing species with buoyant propagules, support our conclusion that surface-related traits operate synergistically with other features, rather than acting alone, in determining dispersal success.

H3. Functional differences between normal and trapped seeds

Our third hypothesis (H3) proposed that trapped seeds differ functionally from normal seeds, with buoyancy shaped by unique trait interactions. Fig. 5j, k support H3, showing opposite relationships between mass and sinking in the two seed types. Greater mass increased sinking probability in trapped seeds (Fig. 5j) but decreased it in normal seeds (Fig. 5k). Normal seeds floated longer, likely due to their flatter shape and enhanced exploitation of surface tension, while trapped seeds sank faster, especially when thin and light. These results indicate functional divergence between normal and trapped seeds, with trapped seeds potentially benefiting from delayed release within capsules, allowing hydrochorous transport even when individual seed buoyancy is low. Nevertheless, many trapped seeds remained afloat for several hours to days long enough to be carried by floods or ice. Their retention within capsules may further enhance dispersal, as floating fruits can transport seeds before gradual release (Lhotská and Kopecký 1966; Fryirs and Carthey 2022).

Najberek et al. (2020) showed that variation in seed-coat traits among populations of *Impatiens glandulifera* affects flotation, supporting the idea that structural divergence among seed morphs, such as between normal and trapped seeds of *E. lobata*, may be an adaptive response influencing dispersal. These findings are consistent with a broader literature showing that heteromorphism or dimorphism in seeds enhances colonization opportunities. Fumanal et al. (2007) reported that heavy and light morphs of *Ambrosia artemisiifolia* seeds differ in dormancy and dispersal, favouring both persistence in soil and rapid colonisation. Likewise, Vander Wall et al. (2005) emphasised that seeds protected from predators or retained within fruits can profit from secondary vectors, including hydrochory, to extend their spatial reach. Findings of Jansson et al. (2005) show that flood-mediated propagule transport promotes recruitment and suggest that traits like seed trapping in *E. lobata* fruits help seeds benefit from hydrochory despite differing flotation capacities.

Implications for hydrochorous dispersal and invasiveness

Together, our findings reveal that *E. lobata* exhibits a flexible dispersal strategy combining seed flotation with fruit-mediated transport. Even if only a minority of seeds float beyond 24 h, the high fecundity of the species ensures effective hydrochorous spread. Seeds can potentially cover dozens of kilometers within days, consistent with dispersal distances reported for other riparian plants (Boedeltje et al. 2004). Kowarik and Säumel (2008) reported that floating samaras of *Ailanthus altissima* maintained high germination potential after several days on water, emphasizing that seed design and flotation duration interact to influence invasion success. Empirical work on other rivers shows that alien diaspores may drift for a week or more, exceeding 150 km under favorable flow regimes (Fryirs and Carthey 2022). In our study, some seeds floated for over 24 h without loss of viability, implying that viable propagules may reach remote sites if no physical barriers intervene.

Floating fruits or capsules can further prolong dispersal, releasing seeds gradually as they decompose or are moved by wind, ice, or animals. This aligns with the findings of Najberek et al. (2020), who demonstrated that seed-coat adaptations improving buoyancy contribute directly to the invasion success of *Impatiens glandulifera*. This trait portfolio corresponds to theoretical expectations that variability in dispersal potential enhances invasion success in dynamic landscapes (Schupp et al. 2010). Hydrochory, supported by seed dimorphism and occasional fruit-mediated transport, thus plays a central role in the ongoing invasion of *E. lobata* along European river valleys. By producing seeds that differ in floating duration, from long-floating to rapidly sinking individuals, this invasive plant is able to colonize both nearby depositional sites and distant downstream habitats. Hydrochory, supported by seed dimorphism and occasional fruit-mediated transport, thus plays a central role in the ongoing invasion along European river valleys.

Conclusions

This study demonstrates that interactions among seed traits fundamentally determine hydrochorous dispersal in *Echinocystis lobata*, shaping a complex system of complementary pathways that underpin its invasive capacity. The coexistence of morphologically distinct seed types and their functional divergence in buoyancy creates a spectrum of dispersal potentials, from rapid local deposition to long-distance downstream transport. Such trait-based variation expands the species' ecological flexibility, allowing it to exploit multiple hydrological contexts and sustain recruitment under varying flow regimes. These results extend current understanding of functional diversity in dispersal ecology and provide an explanation for the rapid spread of this species in riparian systems. By linking trait interactions with ecological outcomes, the study contributes to broader invasion theory, emphasizing that trait plasticity and dispersal polymorphism jointly enhance colonization success in fluctuating aquatic environments.

From a management perspective, early removal of fruiting plants along watercourses is crucial to reduce propagule input, but interventions should also prioritize sites where floating seeds or fruits accumulate and gradually release seeds, creating dispersal hotspots. Integrating this understanding into applied frameworks can substantially enhance prediction and control efficiency by aligning management actions with the species' dispersal processes, hydrological connectivity, and seasonal dynamics. Management guidelines, such as those prepared for national or ministerial plans (e.g., Chmura et al. 2018), can be refined by emphasizing that seed dimorphism and fruit-mediated transport increase colonization potential and by explicitly accounting for both immediate and delayed seed release. Adaptive strategies should therefore combine early propagule removal with targeted interventions at sites of delayed dispersal. Future research coupling trait-based data with hydrodynamic and landscape models could further improve forecasting and help identify priority zones for coordinated control of *E. lobata* and similar invasive species.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: PM, PC. Data curation: AS. Formal analysis: PC. Investigation: AS. Methodology: PM, PC. Project administration: PM, PC. Resources: PM. Software: PC. Visualization: PC, AS. Writing - original draft: AS. Writing - review and editing: PM, AS, PC.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Functional traits of Echinocystis lobata seeds

Authors: Adam Szulc, Patryk Czortek, Pawel Marciniuk

Data type: xlsx

Explanation note: The table presents key functional traits of *Echinocystis lobata* seeds, including morphological and physiological characteristics. Traits include seed mass, length, width, height, entrapped status, and time of floating.

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