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

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Abstract

Echinocystis lobata is an invasive vine species that successfully colonized riverine habitats in Central and Eastern Europe. Although barochory and blastochory have been considered the main mechanisms of its dispersal, increasing evidence indicates an important role of hydrochory, especially nautohydrochory. The study aimed to determine how morphological features of seeds – mass, thickness, surface area, and entrapment status – affect their ability to float. Results obtained from a generalized mixed-effect model assessing the probability of *E. lobata* seeds sinking showed that seed mass affected their buoyancy depending on thickness and entrapment status: thinner seeds with higher mass were more likely to float. In contrast, heavier, entrapment seeds sank faster. Seed thickness significantly reduced the probability of sink, regardless of other features, while the effect of surface area on buoyancy depends on mass; in the case of lighter seeds, a larger surface area increased the risk of sinking. Trapped seeds differ in the way they are released and the course of dispersion – their structure, despite a more frequent loss of buoyancy with a larger mass, may delay the moment of fruit abandonment and promote colonization during periods of water surges. The observed variability of diaspore features supports a plastic strategy, enabling both hydrochory and barochory, depending on habitat conditions. The ability of seeds to float on water for a long time highlights the important role of morphological and ecological adaptations in the invasive success of *E. lobata*.

Introduction

Invasive plant species often utilize multiple seed dispersal strategies that enhance their ability to colonize new habitats. Long-distance dispersal, often facilitated by human activities, helps them overcome geographic and climatic barriers, increasing ecological success. Dispersal mechanisms such as anemochory (wind), ballochory (explosive release), barochory (spread by gravity) and hydrochory (water) are frequently combined within a single species, boosting adaptability and complicating management. For example, *Impatiens glandulifera*, *Acer negundo*, and *Ambrosia artemisiifolia* use mixed strategies that promote expansion in both terrestrial and aquatic habitats.

Hydrochory, especially nautohydrochory (dispersal via surface water), is key in spreading species across river valleys and into otherwise unreachable areas (Sádlo et al. 2018; Parolin 2005). Lightweight seed capsules can float long distances after detaching from the plant. However, mechanisms influencing hydrochoric transport - like buoyancy and retention - are still not well understood (Carthey et al. 2016). As a result, hydrochory-driven invasions can lead to monodominant stands, replacing native vegetation and disrupting ecological processes such as nutrient cycling and habitat structure.

A notable example of a plant employing multiple dispersal modes is *Echinocystis lobata* (wild cucumber), a North American species from the *Cucurbitaceae* family. Native to the U.S., it thrives in moist habitats like riverbanks and wetlands (Choate 1940; Stocking 1955; Gerrath et al. 2008). In Canada, especially Ontario and Quebec, it is considered a noxious weed (Alex 1998). Introduced to Europe as an ornamental plant in the late 19th and early 20th centuries, *E. lobata* has since spread widely across central and eastern Europe - from Spain to the Russian Pacific coast and north to the Gulf of Bothnia (Probatova 1987; Zając et al. 2019). It is now considered invasive in many European countries (Domin 1942; Heine and Tschopp 1953; Dajdok and Kącki 2003; Tokarska-Guzik 2005; Klotz 2009; Kostrakiewicz-Gierałt et al. 2022).

In Poland, wild populations were first recorded in the early 20th century, likely introduced from both Germany and Ukraine (Tokarska-Guzik 2005). By the mid-1960s, it had established itself in the Polish Carpathians and expanded notably in the following decades. *E. lobata* shows a marked affinity for riverine environments, pointing to hydrochory as a key dispersal pathway (Zając et al. 2011), though early studies did not investigate this aspect in detail.

Studies on *E. lobata*'s seed morphology reveal that seeds fall passively from drying capsules (barochory), while some remain protected in fibrous fruit structures. These protected seeds can remain on the plant for extended periods, potentially dispersing later via wind or water (Silvertown 1985; Dylewski & Maćkowiak 2014). Dylewski et al. (2018) identified a unique defensive trait: approximately 34% of fruits contain additional "trapped" seeds, which are less accessible to rodents, enhancing survival in riparian zones.

Although hydrochory is likely vital to *E. lobata*'s success, fundamental questions remain about its dispersal efficiency and seed transport phases. Seeds may undergo surface floating, immersion, or movement along riverbeds (bythisohydrochory) (Carthey et al. 2016; Lhotská & Kopecky 1966). While most seeds sink, floating seeds can still germinate, extending colonization potential. Earlier research in Czechoslovakia explored buoyancy and transport distances (Slavík & Lhotská 1967), while recent work emphasizes the role of vegetation in seed capture and retention along riverbanks (Chambert & James 2009; Fryirs & Carthey 2022). Beyond hydrochory and barochory, *E. lobata* may also disperse via blastochory (transport by climbing shoots) and potentially through anemochory (e.g., capsules rolling on snow), epizoochory (external animal transport e.g. beavers) and anthropochory. However, these modes remain poorly documented. The combination of diverse dispersal strategies likely explains *E. lobata*'s persistence and expansion, particularly in dynamic floodplain ecosystems. *E. lobata* exemplifies how combining multiple seed dispersal mechanisms facilitates successful invasions. Hydrochory plays a particularly important role in riparian environments, enabling long-distance spread, colonization of disturbed habitats, and resilience against removal. Understanding such complex dispersal systems is essential for managing invasive species and protecting native biodiversity.

In the context of the novel weapons hypothesis (Callaway & Ridenour 2004), which assumes that invasive species succeed due to traits that are unknown or unusual in the ecosystems to which they are introduced, the development of traits by a plant that minimize seed predation (e.g. color mimicry, thorny fruits, dry and unpalatable seed covering tissue) may constitute a new type of defensive "weapon." In secondary ecosystems, where local fauna is not adapted to cope with such strategies, seed predation pressure is reduced, which translates into a higher survival rate of diaspores. Such traits may therefore act as chemical or mechanical novel weapons, leading to disparities in regenerative succession. The invasive plant gains a competitive advantage because its seeds are eaten less often and thus colonize new niches more effectively. increase the range of invasion - especially if they are accompanied by other traits that increase dispersal efficiency (e.g. hydrochory, anemochory). Ultimately, this can lead to habitat homogenization, displacement of native species and destabilization of ecosystem functions.

Callahan and Lincoln (2022) mention seed-eating rodents as dispersal agents but do not consider other mechanisms. Dylewski et al. (2018) observes that some fruits contain additional seed locules, though it remains unclear how this entrapment affects seed buoyancy. Moreover, the functional trait differences between trapped and regular seeds are unknown, prompting this study. The aim is to examine how morphological traits - such as seed mass, thickness, surface area, and shape - jointly influence *E. lobata* seed buoyancy. Rather than analyzing traits in isolation, the study focuses on their interactions and implications for water-based dispersal. It investigates whether smaller seeds always float better or if retained fruit tissues enhance buoyancy. The research explores whether trapped seeds show structural adaptations for delayed release and increased hydrochory. Another goal is to assess how morphological variability helps *E. lobata* adapt to changing hydrological regimes and whether seed thickness can offset mass to maintain flotation. The study also evaluates how the coexistence of trapped and normal seeds affects dispersal timing and synchronization with environmental cues. Finally, it considers if greater investment in seed quality - particularly buoyancy and post-submersion germination - offers an advantage over high-output propagule strategies.

Therefore, we hypothesized that: H1: Seed mass significantly influences the probability of sinking, particularly through its interaction with seed thickness and size; H2: Seed surface area (size) affects flotation potential primarily when interacting with seed mass, but has limited independent effect; H3: Trapped seeds differ functionally from normal seeds, and their sinking probability is shaped by unique interactions between seed mass, size, and thickness. These hypotheses were formulated to reflect the role of complex trait interactions in shaping the hydrochoric potential of *E. lobata* seeds under variable environmental conditions.

Material and methods

Study area

Six populations of *E. lobata* distributed in Poland in the Bug and Liwiec river valleys were selected for the study. Four sites are located in the river Bug valley, three of which are in the Lower Bug Valley mesoregion (Skuszew [52.597541, 21.496463], Szumin [52.605591, 21.630354], Wywłoka [52.617024, 21.677217]) and one in the Podlasie Bug River Gorge mesoregion (Drażniew [52.373972, 22.709384]) (Kondracki 2002). Two sites are located in the Liwiec river valley. The Liwiec River is a left-bank tributary of the Bug River, and *E. lobata* sites are located near its mouth (Koszelanka [52.560705, 21.599272]) and (Barchów [52.512139, 21.642357]). These sites are located in the transition zone between the Lower Bug Valley and Wołomin Plain mesoregions. All sites are located in the zone of annual flooding associated with spring floods and rarer floods after heavy summer rainfall.

Seed measurement methods

We examined normal and trapped seeds and seed buoyancy from both groups. Due to the planned experiments with seed buoyancy, we decided not to collect abnormally formed seeds. We measured the following functional characteristics of seeds: length, height, thickness in millimeters, and fresh weight in grams.

We calculated the seed surface area (mm^2) - the shape of *E. lobata* seeds resembles an oval, so we used the formula for the surface area of an ellipse [πab] where a and b are the semi-axes of the ellipse, in the case of seeds half the value of length and width. We also calculated the seed shape coefficient by dividing the width of the seeds by their length. A product result of less than 0.5 indicates that the seeds have an elongated lanceolate or oval shape and are at least twice as long as they are wide. A result greater than 0.5 indicates an oval to spherical shape.

We collected the fruit in October and November 2024. After harvesting, selection was made into fruits containing trapped and normal seeds. We collected normal seeds separately. Capsules containing trapped seeds are easy to distinguish from normal ones. You should shine a flashlight on the fruit and look into the chamber. A trapped seed will shine through the walls of the chamber. To extract trapped seeds, you should carefully cut the fruit with a scalpel. Each seed was given its number and envelope, which we stored in plastic containers. We measured the fruits and seeds with a Yato YT-7201 electronic caliper and weighed them with a Steinberg SBS-LW-500 laboratory scale. After measuring the seeds, we experimented to determine their ability to nautohydrochory and the time it took to sink. The seeds were stored in a roofed room in outdoor weather conditions throughout the period from harvest to the experiment. The experiment was also carried out outdoors, at temperatures that prevented ice from forming in the containers with water (between 1 and 7°C). We measured the number of floating seeds at 24-hour intervals for 14 days. We threw the seeds, each separately to avoid confusion, into a container with water. We transferred the floating seeds to numbered test tubes with water that allowed them to float and to observe the time it lasted.

Statistical methods

To evaluate the importance of hypothesized seed traits in shaping the probability of the *E. lobata* seeds sinking, we fitted a generalized mixed-effect linear model assuming the binomial distribution for the response variable implemented in the *glmmTMB::glmmTMB()* function (Brooks et al. 2017). The model included five interaction terms among five predictors. We examined how seed mass influenced seed area and accounted for the effects of seed thickness on seed mass. Furthermore, we assessed the effects of seed trapping status (trapped vs. normal) on seed area, seed thickness, and seed mass.

To account for potential variation in seed traits among *E. lobata* populations of different origin, we included the study site identity as a random effect in the model performed. Using the *MuMIn::r.squaredGLMM()* function (Bartoń 2024), we calculated marginal (R^2_m) and conditional (R^2_c) coefficients of determination to quantify the variance explained by fixed effects alone and by both fixed effects and the random factor, respectively. The difference between R^2_c and R^2_m corresponds to the variance attributed specifically to the random effect.

In interpreting the model results, we placed greater emphasis on effect sizes than on *P*-values. This decision aligns with increasing concern that *P*-values, due to their sensitivity to sample size, may fail to reflect biologically meaningful patterns if assessed solely (Wasserstein & Lazar 2016). We illustrated the model results by visualizing marginal responses, i.e. predicted values assuming effects of all other explanatory variables are held constant, using the *ggeffects::ggpredict()* function (Lüdecke 2018).

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Results

To investigate the influence of seed characteristics on their ability to nautohydrochory in *E. lobata*, we conducted a buoyancy experiment on 1362 seeds. We divided the seeds into normal and trapped. The proportion of floating normal seeds was 12.3%, and trapped 17.8%. After the first day, 31.1% of trapped seeds and 12.3% of normal seeds floated. After 48 hours, the proportion of floating trapped seeds dropped to 0.7%, and normal seeds to 2.6%. Trapped seeds sank faster (up to 11 days), while normal seeds remained up to 14 days.

We found that all hypothesized predictors together explained 43% of the variance in the probability of seeds sinking, while study site identify (random effect) accounted for only 11% of the variance (**Table 1**). An effect of seed size on the probability of sinking was markedly influenced by seed mass (**Fig. 1a-c**). For lower-mass seeds (≤ 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. 1a**). 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. 1b**), 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. 1c**). The relationship between seed mass and the probability of sinking was subtly influenced by seed thickness (**Fig. 1d-e**). For thin *E. lobata* 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. 1d**). For thicker seeds (> 0.30 cm), it decreased from 52% at a mass of 0.12 g to 0% at 0.52 g (**Fig. 1e**). The relationship between seed size and the probability of sinking was only slightly affected by trapping status (**Fig. 1f-g**): in trapped seeds, the probability of sinking increased from 3% at 0.20 cm^2 to 42% at 0.80 cm^2 (**Fig. 1f**), while in normal seeds it increased from 1% at 0.20 cm^2 to 31% at 0.80 cm^2 (**Fig. 1g**). We observed a similarly gentle effect of trapping status on the relationship between seed thickness and sinking probability (**Fig. 1h-i**). For trapped seeds, the probability of sinking decreased from 98% at 0.24 cm thickness to 0% at 0.51 cm (**Fig. 1h**), whereas for normal seeds, it decreased from 65% at 0.24 cm thickness to 0% at 0.51 cm (**Fig. 1i**). The relationship between the probability of seed sinking and their mass was strongly affected by the trapping status (**Fig. 1j-k**). For trapped seeds, it increased from 1% at a mass of 0.06 g to 57% at 0.52 g (**Fig. 1j**), while for normal seeds, it decreased from 82% at a mass of 0.06 g to 0% at 0.52 g (**Fig. 1k**).

Table 1. A generalized mixed-effect linear model of *E. lobata* seeds sinking probability depending on seed traits and trapping status (AICc = 791.8; $AICc_0$ = 1052.1). RE – SD of random effects.

Predictor	**Estimate**	**SE**	**z**	**Pr(>|z|)**	**RE SD**	R_m^2	R_c^2
(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			

Figures

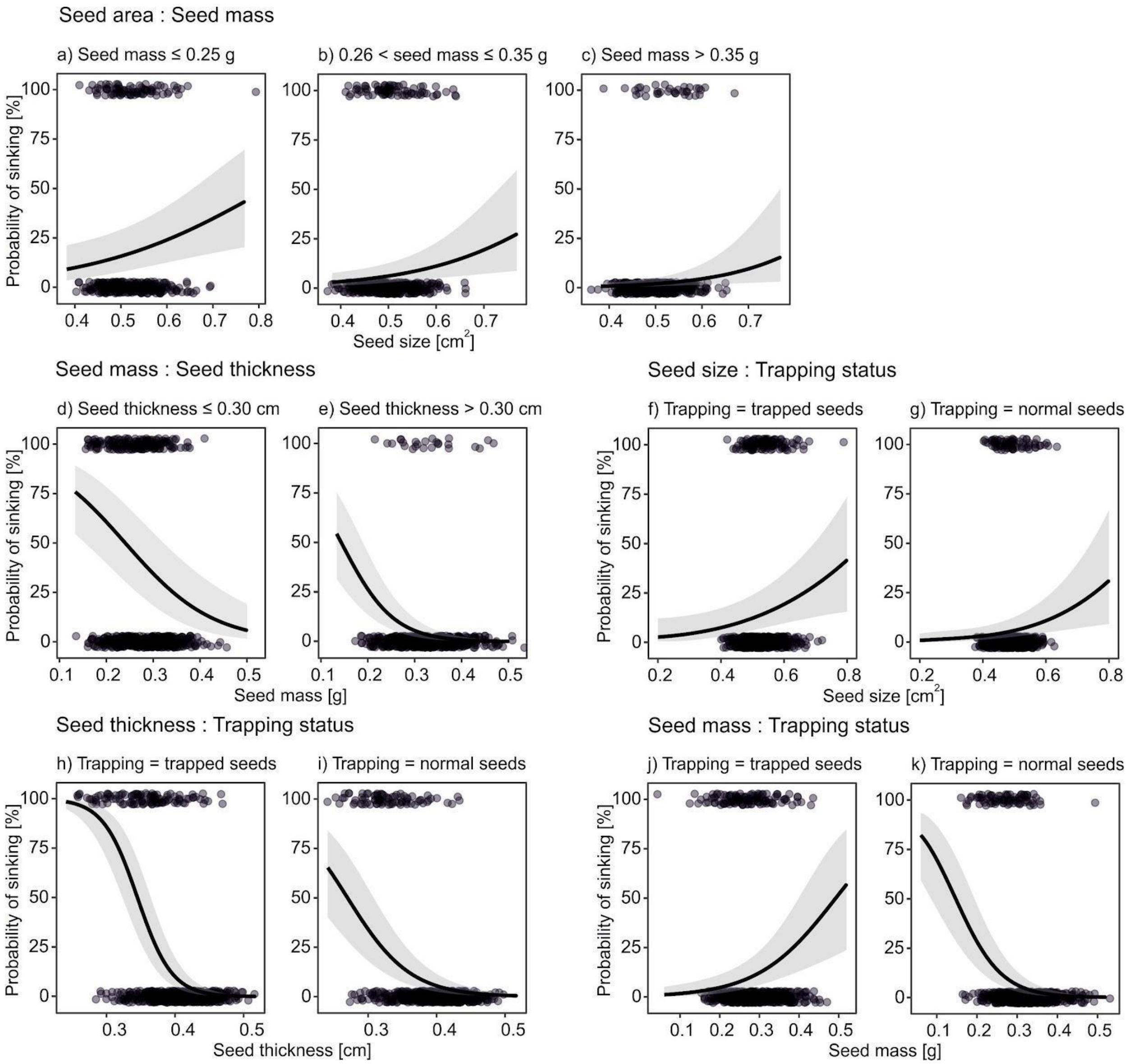

Fig. 1. Marginal responses of *E. lobata* seeds sinking probability, estimated using a generalized mixed-effect linear model (**Table 1**).

Discussion

Due to the large mass and thickness of the seeds, it was hypothesized that these features affect their buoyancy – lighter and thinner seeds float more easily, while heavier ones sink more quickly. Shape also plays a role – flattened, streamlined seeds can better distribute their weight in the water, increasing buoyancy, while spherical seeds sink more quickly. The results showed that both mass and size affect buoyancy. At low and medium masses, larger seeds were more likely to sink. Heavy seeds were the least likely to sink, especially with a smaller surface area (only 1% sank). The relationship between features is not linear; mass can stabilize buoyancy when combined with the right size. Thicker and heavier seeds are less likely to float because their mass exceeds the buoyancy force, leading to sinking. Thicker seeds have a higher density and a smaller surface area relative to their mass, which reduces their buoyancy. Thinner and lighter seeds, on the other hand, make better use of the surface tension of the water, making them easier to stay afloat. This affects their ability to disperse in the aquatic environment. The seed mass exhibited significant variability, which may facilitate adaptation to diverse environmental conditions. Studies (Lopez 2001) show that seeds from flooded forests have a larger volume and lower specific mass, which increases buoyancy. The opposite is true in non-flooded forests. Similar results are obtained by Carthey and Ralph (2022), who state that seeds with higher density sink faster. Broek et al. (2005) confirm that seeds from humid environments have higher buoyancy and are more effective in dispersing with water. Heavy, trapped seeds floated better than heavy, normal seeds; for the first 24 hours, the percentage of floating seeds was higher. These differences result not only from mass, but also from thickness – the thicker the seeds, the greater the risk of sinking. In thin seeds, we observed the opposite relationship: greater mass reduced the probability of sinking. This effect was stronger in thin than in thick seeds. The result that for thin seeds, increased mass reduced the probability of sinking is surprising, because we would normally expect that increased seed mass increases seed density, which leads to faster sinking. However, for thin seeds, increased mass may improve their buoyancy by increasing their buoyancy, allowing them to float longer. This effect was stronger for thin seeds than for thick seeds, suggesting that the interaction between seed mass and thickness affects their ability to float. This result indicates the importance of the interaction between seed mass and thickness in shaping their ability to float. Thin seeds with a higher mass may float longer, which increases their chances of being transported over long distances and colonizing new areas. In contrast, thick seeds, despite their higher mass, may sink faster, which limits their ability to disperse in water. The hypothesis was confirmed, the interaction of seed mass, thickness, and surface area affects their buoyancy, which is crucial for the dispersion of *E. lobata* seeds in aquatic environments.

The second factor influencing sinking was the size of the seed surface. We investigated how this feature affected the probability of sinking in trapped and free seeds. For trapped seeds, increasing the surface area increased the probability of sinking. In contrast, for free seeds, such an increase in surface area had no significant effect. This indicates that trapped seeds were more likely to sink at larger sizes. Chambert and James (2009) note that larger seeds are more likely to move farther, among other things due to their ability to avoid obstacles and less prone to getting stuck in vegetation. However, in the context of buoyancy, seed surface area plays a role mainly in the interaction with mass. Hypothesis H2 was confirmed. Seed surface area affects buoyancy mainly in the interaction with seed mass, which is important for the dispersal strategy of *E. lobata*. We observed a similar effect distinguishing trapped seeds when analyzing the relationship between thickness and sinking probability. For thin, trapped seeds, 98% of them sank, while thick seeds did not. Normal seeds were less likely to sink, but thick seeds did not sink either. This shows that increased thickness protects seeds from sinking regardless of whether they are trapped or normal. However, trapped seeds were much more likely to sink at lower thickness. Seeds trapped in water may be more likely to sink at lower thickness due to their larger surface area relative to volume. According to Carthey and Ralph (2016), small, irregularly shaped seeds with larger surface area may be held afloat by surface tension, which allows them to avoid sinking. However, if the surface area of the seeds is too small relative to their volume, the surface tension may not be sufficient to keep them afloat, leading to their sinking. Additionally, thinner seeds may absorb water more quickly, which increases their density and accelerates the sinking process. In the context of captive seeds, their larger surface area relative to volume may make them more susceptible to the effects of surface tension, which may lead to them being retained on the water surface. However, if their shape and structure do not facilitate the efficient use of surface tension, they may sink more quickly. The reduced thickness of captive seeds may lead to their greater susceptibility to sinking, especially if their surface area is not large enough to effectively utilize the surface tension of water.

Captive seeds were much more likely to sink at a lower thickness, primarily due to an unfavorable relationship between mass, density, and supporting surface area. A thin shell means less structural rigidity and often a smaller volume of air retained in the tissues, which reduces buoyancy. In the case of captive seeds, which are additionally packed into a limited space of the fruit, this may result in a less favorable surface-to-mass ratio, which promotes sinking. In the study by Carthey et al. (2016), it was indicated that features such as low thickness, high density, and the lack of structures increase resistance in water (e.g. hairs, wings) strongly limit the ability of seeds to float. This is also confirmed by the results of Fryirs & Carthey (2022), who noted that smaller seeds with a smooth surface and without adaptations for swimming were more likely to sink faster, especially if they did not have air-retaining structures. In the case of *E. lobata* captive seeds, their thin shell may not have provided sufficient buoyancy or protection against rapid water uptake. Lack of access to light in the developing fruit tissue may also have limited their morphological and functional development. Such seeds, lacking highly porous tissues or air spaces, absorb water more quickly, leading to faster sinking. Thin-walled, captive seeds have lower buoyancy due to their smaller relative volume, lack of buoyancy-supporting structures, and faster water uptake. This makes them more susceptible to sinking and limits their effectiveness in long-distance hydrochory unless they are dispersed with the entire fruit, which may partially compensate for these limitations.

The last aspect analyzed is the relationship between mass and probability of sinking, divided into normal and trapped seeds. For trapped seeds, the greater the mass, the greater the probability of sinking. For normal seeds, the relationship was the opposite. Greater mass improved the ability to float only in normal seeds. For trapped seeds, greater mass increased the risk of sinking. The effect of mass on sinking was therefore strongly dependent on the type of seed. Thickness and mass had the greatest effect on sinking, while the size and type of seeds had a smaller but still significant effect. An exceptionally strong relationship concerned thin and light seeds – they were most susceptible to sinking. On the other hand, normal seeds had the best floating properties: thick and heavy. Whether a seed sinks depends not only on one feature, but on the interaction of several parameters. The experiment showed that the relationships between the physical features of seeds are complex and interconnected in both seed groups. Hypothesis was confirmed. The captive seeds of *E. lobata* are functionally different from normal seeds, and their buoyancy is shaped by unique interactions of physical features, which influences their dispersal strategy and potential invasiveness. On average, normal seeds are heavier than captive seeds, which results from the possibility of freer growth in the larger space of the seed chamber. Captive seeds grow in a confined space, which results in their smaller size. We observed that some normal seeds penetrate the distal coat, escaping from the chamber before falling out. Captive seeds float better and have a greater chance of reaching water during autumn and winter floods. Dried capsules with such seeds can float on water or be carried on ice, and seeds fall out through fruit pores. We also observed their transport by beavers on the shoots of cut riverine shrubs. *E. lobata* uses two main dispersal strategies: barochory and hydrochory, mainly nautohydrochory. The greatest variation in seed size occurs in captive forms. Large seeds have longer hypocotyls, which allows them to germinate from greater depths, which is important in flooded environments. They also contain more reserve substances, which supports seedlings at the start and reduces competition. However, plants producing large seeds produce fewer seeds. *E. lobata* produces an average of 28 fruits (ca. 112 seeds), with a seed distribution of 3 to 77 fruits per plant (Slavík & Lhotská 1967). The larger surface area and smaller mass reduce the pressure exerted on the water, which promotes buoyancy. In turn, heavier seeds with a smaller surface area sink faster due to the greater pressure per unit area. The differences in volume were surprising - seeds with a larger volume sank more often, probably because of their greater mass. The seed coat of *E. lobata* is hard, smooth, or slightly rough, without structures increasing the surface area or retaining air, which limits buoyancy. There are also no elements that aid in lifting, as in the seeds of Bidens sp. or Impatiens glandulifera.

We also showed the influence of shape on buoyancy – seeds with a higher width-to-length ratio float better. Shape influences the distribution of pressure in water – more flattened seeds float better, while spindle-shaped ones sink quickly. The trapped seeds likely serve as a reserve inside the fruit and float for a shorter time due to their more spherical shape. Normal seeds that fall to the ground are more likely to be eaten or buried by alluvial material, but they float longer and have a greater chance of water dispersion. Even if only 10% of seeds float for more than 24 h, given their large numbers, this explains the rapid expansion of the species. Fryirs et al. (2022), after examining 60 riverine species, finds that half of the seeds sink within 2 days and 90% within a week. Seeds of alien species float longer, 40% more than a week, which facilitates their dispersal. The potential drift distance of seeds is up to 21 km per day, or even 150 km per week. The seeds of *E. lobata* in our study floated for at least 24 hours without losing their germination capacity, depending on the location, 10% to 80% of the seeds floated. In rivers with a sandy bottom, some seeds are buried, others drift, or are stopped by obstacles. When they do not encounter barriers, they can cover up to 330 km per week at a river speed of 2 km/h. However, in recent years, the lack of floods may limit dispersion, which makes it difficult to colonize the lower sections of rivers. The time of seed floating on the water has been studied in many river species. *Cyclachaena xanthiifolia*, an invasive species from North America, is characterized by heterocarpy and develops two types of seeds. Smaller ones sink after 12 h, are lighter, have an elongated shape, a small surface area, and are moderately flattened. The larger ones float for 24 h, are heavier, wider, strongly flattened, have a large surface area, and have a wide rim (Lhotská et al. 1969). This confirms the influence of surface area and shape on buoyancy. Some species disperse through floating fruits. In *Euphorbia adenochlora*, floating schizocarps can burst, throwing seeds up to 4.1 m away (Niwa 2024). As many as 33% of coastal populations come from such ballochory. In *E. lobata*, dried fruits can also float on water, carried by wind, beavers, or ice. The seeds contained in them (especially those trapped) can be released after the fruit decomposes. Nautohydrochory enables the colonization of new places by stopping floating seeds in coastal zones. Seeds can also be carried across the valley. Floodwaters flood higher areas, and water recedes through oxbow lakes and tributaries, allowing them to move. Oxbow lakes often connect to the mainstream only in the lower part of the former channel. The backwater also facilitates this transport.

The seed buoyancy time in our study was longer than previously reported in the literature, suggesting a higher than expected efficiency of this dispersal mechanism. Studies have shown that the buoyancy of *E. lobata* seeds is a complex function of the interaction of several morphological features – primarily mass, thickness, surface area, and shape. Their influence is not linear, and the significance of individual parameters varies depending on the type of seed (normal/trapped):

- Mass and thickness have the greatest influence on buoyancy. For thick seeds, greater mass promotes sinking. On the other hand, for thin seeds, greater mass can increase buoyancy, which is a surprising effect, but important for understanding the mechanisms of water dispersion.

- Surface area affects buoyancy mainly through interactions with mass; in light seeds, greater surface area increases the risk of sinking. In trapped seeds, a large surface area reduces buoyancy more than in normal seeds.
- Seed shape, more flattened forms float better on water than spherical ones, which may increase their range.
- Trapped seeds, although they sink more often, are effectively dispersed. Their ability to float for several dozen hours may be sufficient to colonize distant locations under favorable hydrological conditions.

Conclusions

1. The buoyancy of *E. lobata* seeds is the result of complex interactions of morphological features such as mass, thickness, surface area, and shape. The influence of each of these features depends on the values of the others, which confirms the importance of their interaction in shaping the ability of seeds to float on water.
2. The role of seed mass is dependent on other features:

a. For thinner seeds (≤ 0.30 mm), increasing mass significantly reduces the probability of sinking.

b. For trapped seeds, on the contrary, it increases the risk of sinking. This means that mass does not act alone, but in interaction with thickness and entrapment status.

3. The thickness of the seeds is crucial for their buoyancy. For both normal and trapped seeds, increased thickness significantly reduces the probability of sinking – this effect is more pronounced in trapped seeds.
4. The surface area of the seeds affects their buoyancy depending on their mass. In lighter seeds, increasing surface area is associated with a higher probability of sinking, while in heavier seeds, this effect is less pronounced. This shows that a large surface area does not always promote buoyancy – its effect depends on the seed mass.
5. Trapped seeds differ in their dispersal mechanism. Although they often show a higher risk of sinking with a larger mass, their structure (e.g., the presence of fruit debris) may delay release and allow dispersal during seasonal floods. Their buoyancy is not always higher, but their dispersal strategy may be more adapted to the environment.

6. High variability of seed traits, such as mass, thickness, and surface area, may be an adaptation enabling the use of different dispersal strategies: barochory and hydrochory. This allows *E. lobata* to occupy different ecological niches in riverine habitats.
7. Seed type (normal vs. trapped) influences the relationships between traits and buoyancy. The interactions between mass, thickness, surface area, and seed type (trapped vs. normal) are statistically significant and indicate differences in the behaviour of the dispersals concerning water. The ability of some seeds to float for long periods and to germinate after submergence supports the successful colonization of river valleys and alluvia. The mechanism of nautohydrochory plays an important role in the invasiveness of *E. lobata* in European environments.
8. Comparisons indicate that principles of seed ecology, such as the relationship between specific mass and surface area, are universal in seasonally flooded ecosystems. E. lobata fits into this pattern through the morphological plasticity of its seeds.
9. Instead of investing in large numbers of diaspores, E. lobata develops complex seed traits, such as variable buoyancy and delayed dispersal. This strategy reduces seedling competition while increasing colonization success.

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