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Source effects determine hydrochorous seed dispersal of ancient forest plants

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Abstract Plant species of ancient forests tend to be poor dispersers, but recent field studies suggest that dispersal may be strongly accelerated in streams. To further test this idea, we addressed the following two questions: (1) which traits facilitate transport and deposition of seeds by streams? (2) do ancient forest species differ from other forest species with respect to these traits?. In the Boven Slinge, a forested lowland stream in the Netherlands, we measured seed transport and deposition and analysed which traits best explained this. We subsequently compared ancient forest species with other forest species with respect to these key traits. Our field measurements indicated that stream dispersal is determined by both source- and path-related processes. Significance of upstream population size, seed production and seed release period mirrored source effects, whereas significance of buoyancy and seed mass indicated that the path, i.e. stream transport and deposition, further constrains the number of species that can be dispersed by streams. Compared to other forest species, ancient forest species do not differ with respect to seed release period, buoyancy and seed mass, but at a given plant height, ancient forest species produce less seeds than other forest species. This may reflect an adaptation to their relatively stable habitat which comes at the expense of (stream) dispersal capacity. In conclusion, ancient forest plants are just as well equipped for stream dispersal as other forest species, but success will critically depend on upstream population size, given their low per plant seed production.

Keywords Ancient forest · Hydrochory · Seed dispersal · Stream dispersal

Introduction

In many plant communities, environmental variability is the main factor determining species composition (Silvertown et al. 1999). Recently, it has become recognised that differences in colonising ability may also play an important role. This has clearly been demonstrated for temperate forests, where species strongly differ with respect to the speed with which they manage to colonise old fields or set-aside managed forests (Verheyen and Hermy 2001; Naaf and Kolk 2015; Litza and Diekmann 2019). Peterken (1974) and Hermy et al. (1999) have distinguished species of secondary forests and 'ancient forest species'. The latter group has a strong affinity for forests at least 150 years old. These species tend to be more shade tolerant and have a narrower range of moisture, pH and nitrogen preference than species that also thrive in young forest, hereafter referred to as 'general forest species'. Although abiotic conditions may be inadequate in young forests (Honnay et al. 1999; Baeten et al. 2009), ancient forest species are also lacking in younger forests that match their ecological optima (Verheyen and Hermy 2001; Baeten et al. 2010; Brudvig et al. 2011).

This is most likely a consequence of dispersal limitation since 75% of ancient forest species either lack any adaptation to dispersal or rely on animal-mediated dispersal (Hermy et al. 1999). The latter usually results in short dispersal distances since many forest animals have a restricted home range (Brunet and von Oheimb 1998;

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Hermy et al. 1999; Bossuyt et al. 1999). However, ancient forest species may also be dispersed by streams, and studies have shown that this may strongly accelerate dispersal rate and population exchange between remote suitable downstream forest patches (Honnay et al. 2001; Araujo Calçada et al. 2013; Holeštová and Douda 2021).

In this study, we addressed the question whether stream dispersal can overrule differences in colonizing ability between general and ancient forest species. To answer this, we took both source and path effects into account (sensu Schurr et al. 2008). Source effects in relation to stream dispersal refer to the amount of seeds available for dispersal, which depends on upstream population size, per plant seed production (Boedeltje et al. 2003) and seed release period (Boedeltje et al. 2004; Greet et al. 2012). Path effects in this context refer to transport and deposition by the stream. Earlier work has identified seed buoyancy and seed mass as key traits for the path (Boedeltje et al. 2003; Nilsson et al. 2010; Carthey et al. 2016).

The value of both source- and path-related traits may critically depend on environmental context. A high seed production in an upstream forest plant population only results in abundant stream dispersal if seeds can enter the stream through runoff or flooding of the forest floor. This requires higher discharges in the stream, coinciding with seed release period (Merrit and Wohl 2002). Long floating seeds will be easily transported and deposited by the stream, but displacement of heavy, non-floating seed critically depends on stream power (Merrit and Wohl 2002; Gurnell et al. 2008; Carthey et al. 2016; Fraaije et al. 2017).

We evaluated the potential for stream dispersal of general and ancient forest species in two consecutive steps. First we used a field sampling design to identify which source- and path-related traits affect transport and deposition by the stream. This was done by measuring seed transport in a semi-natural forested stream at various discharges and measuring seed deposition by this stream at different elevational positions of the riparian zone. The seeds were identified to species level and trait values of these species were used to identify key traits. To ensure a wide trait space, we included all species, i.e. also the open habitat species, found in our samples.

In our second step, we performed a desk study. Here, we tested whether the ancient forest species differ from general forest species with respect to one or more of the key traits identified in our field study. This desk study was not constrained to the forest species found in our samples but included all forest species for which trait values were available, either from trait data bases or own measurements. We thus tried to reach a more general conclusion on the potential of general and ancient forest species for stream dispersal. Since forest species include understorey herbs, shrubs and trees, we applied allometrical relations (Weiner et al. 2009) when comparing both groups for height-related traits.

Materials and methods

Study area

From April 2014 to April 2015, the study was conducted in the Boven Slinge, a lowland stream in the Netherlands. The stream is 20 km long, and at our sampling sites, its slope is approximately 0.84 m/km, with a width of 5 m at median discharge. The stream has a naturally meandering course, characterized by woody debris and tranquil reaches intersected by rapids.

The stream valley upstream from our sampling points includes the Natura 2000-reserve *Bekendelle* and mainly consists of natural, unmanaged deciduous forests. Occasionally flooded parts are characterized by *Alnus glutinosa-Fraxinus excelsior* forests, whereas *Quercetea* and *Querco-Fagetea* forests characterize the higher elevated stretches along the stream. In our mainly shaded stream, submerged species were usually absent, but locally abundant in open stretches together with emergent aquatics that occurred in ribbon-shaped patterns in the lower riparian zone. Various mud-flat pioneers also thrived in open stretches, more specifically at sandy and silty deposits that emerge above water surface at low discharges. In the higher elevated riparian zone, tall herb species dominated non-forested patches.

Discharge fluctuates in response to rain and, over a year, water levels are generally highest in autumn, winter and early spring (Online Resource 1). In the research period, it varied from 0.04 $m^3.s^{-1}$ to a maximum of 5.2 $m^3.s^{-1}$, which is, on average, exceeded 4 days a year. At base discharge, i.e. the value exceeded 95% of the year, flow velocity is approximately 0.15 $m.s^{-1}$.

Field study: sampling of water transport

Water transported diaspores (i.e. generative and vegetative dispersal units) were sampled using an exchangeable net (mesh size 200 μm) with an opening measuring 100 × 40 cm and a length of 200 cm embedded in a stainless-steel frame. If discharge and flow velocity were high, the net device was placed in the middle of the stream by suspending it to a steel frame, attached to a bridge (51°56′32.6″ N, 6°41′29.3″ E; Online Resource 2). At low discharge, the net was placed between stones near the bridge, where flow velocity was sufficient for water to pass through the meshes of the net. Samples were collected semimonthly during the period April 2014–April 2015. The length of a sampling period was usually 0.5 h but its precise duration was determined by the amount of drifting material and suspended matter in the water which could block the meshes of the net (cf. Boedeltje et al. 2003). Five or (during peak discharges) six subsamples were collected in succession at a sampling day. Counts of subsamples taken at the same day were later pooled to obtain one sample per day. In total, 127 subsamples were collected, spread over 25 days.

Flow velocity was measured simultaneously using a flow rate meter attached to a rod next to the net. In addition, the surface of the net opening under water was recorded. The product of flow velocity, surface of the net opening and duration of sampling provided an estimate of the total volume of water that had passed the net in each sample.

Field study: sampling of water deposition

Deposition of diaspores was measured using 50 × 50 cm polyethylene astroturf mats as traps. Three mats were fastened with wing nuts to a water-repellent multiplex plank which was placed at an angle of 30° in the water body, perpendicular to the stream bank (Online Resource 3). The lowest mat was placed at an elevation (ca 27.9 m N.A.P) where it would be flooded at average water level in summer. The second and third mat were fastened 25 cm and 30 cm higher. During the sampling period, low, middle and high elevated mats experienced a total flooding duration of 222, 25 and 5 days, respectively. The high elevated mats were flooded in December 2014 and January and March 2015 (Online Resource 1), mats in the middle also in November 2014 and February 2015.

This design was replicated 10 times by installing 10 such planks in longitudinal direction along the stream at similar elevational position and with a minimum distance of 10 m between planks. From April 2014 until April 2015, mats were regularly retrieved and replaced by clean mats. We aimed to replace them monthly, but in January and February, the lowest mats could not be retrieved due to complete submergence.

Field study: processing of the samples

Net samples were washed out and subsequently hand-sorted, using a white bin in the field. Dead material was removed and vegetative parts larger than 0.5 cm were separated from seeds and smaller vegetative structures. All viable plant parts were taken to the greenhouse for further processing.

Mats were, after retrieval, put in a plastic bag and transported to the greenhouse, where they were washed out on a sieve (0.200 mm mesh width) while removing and collecting large vegetative plant parts. The fine material remaining on the sieve was further analysed on amount of viable diaspores**.**

Large vegetative diaspores from net and mat samples were tested for viability by planting them in wet potting soil under greenhouse conditions. Diaspores that formed roots and/or leaves were considered viable. Seeds and small vegetative fragments of each sample were spread out in a thin layer (< 5 mm) in trays filled with a mixture of equal parts of sterilized sand and potting soil and set to germinate in a greenhouse under moist conditions (water level 8 cm below soil surface) for 3 months. Air temperature in the greenhouse was 20–25 °C between 0600 and 2100 h (photoperiod) and 15 °C between 21.00 and 06.00 h. After this germination period, the trays were placed moist in a dark room at 5 °C during ten weeks to break dormancy (Baskin and Baskin 2014). Thereafter trays were set to germinate again for 3 months, under similar conditions as in the first run. Emerged seedlings were counted and removed as soon as they could be identified. Except *Callitriche* and *Betula,* all seedlings could be identified to species level.

Although our processing of samples will have been adequate to retrieve the majority of species (Boedeltje et al. 2003; Baskin and Baskin 2014), it may have overlooked seeds of bulbiferous species, such as *Galanthus nivalis* or *Gagea lutea* which require a different temperature regime for root or cotyledon emergence (Kondo et al. 2004; Newton et al. 2015).

We counted plants emerging from both generative and vegetative diaspores. However, diaspores in both our water transport and deposition samples were mainly generative. In our net samples, 97.8% of the plants emerging in the greenhouse originated from seeds, whereas 86.7% of the diaspores on mats were generative. Our analyses and reports hereafter are therefore constrained to seeds.

Field study: traits and environmental factors

We use the term trait for both functional traits and features of species specific for this study, such as upstream occurrence. Upstream occurrence of all vascular plant species was recorded in a 4.5 km stretch (including three small tributaries) immediately upstream of sampling points, in March, May and July 2014 and 2015. The stretch was subdivided in 100-m long sections, 10 m wide at each side of the stream. This 2 × 10 m wide zone was assumed to encompass the entire area in which seeds might reach the stream. In each section, the presence and abundance of each species were recorded. In total, 45 100-m sections were surveyed within the main stream and 16 within the tributaries. For our analyses, we derived from these data: frequency (proportion of sections in which a species occurred), total abundance (sum of abundance for all sections) and minimum distance, i.e. from the sampling point to the middle of the nearest upstream section where the species occurred. Nomenclature of vascular plants is according to Duistermaat (2020). Since water transported seeds were sampled 1,5 km upstream from the point where water deposited seeds were sampled, upstream occurrence for species was also determined on a partly different trajectory of the stream. As a consequence, species values for upstream occurrence slightly differed for analysis of transport and deposition.

The time it takes for 50% of the seeds to sink was taken as measure for buoyancy. Data gathered by Boedeltje et al. (2003) were used, supplemented with additional measurement of buoyancy on 113 species. Other trait data were obtained from the LEDA-traitbase (Kleyer et al. 2008), the D3-traitbase (Hintze et al. 2013) and Grime et al. (1989). These were seed mass, seed production per plant and release period, i.e. the period (in months, within the range 1–12) during which mother plants may disperse seeds. Seed buoyancy and seed mass refer to the entire generative dispersal unit, i.e. including fruit tissue or attachments such as wings or plumes.

A continuous water level recorder located immediately downstream from our deposition mats provided water discharge information. Data on wind velocity and precipitation in the research area were provided by the Weather Station Hupsel (www.logboekweer.nl).

Field study: Correction for airborne seeds on the mats

As our interest focused on water-borne seeds, we used the number deposited on the highest mats as controls for wind or animal-deposited seeds, provided that mats were not flooded before being sampled (Online Resource 1). For each species, this number was subtracted from the number of seeds deposited on the (flooded) middle and low elevated mats of the same plank. In December, January and February, the highest mats were also flooded so for these months correction for airborne seeds was not possible. Since these winter months are outside the seed release period of most species, it is unlikely that airborne seeds will have influenced our deposition measurements.

Field study: statistical analyses

All vascular plant species occurring upstream were included in the analyses, except ferns, horsetails and orchids whose spores and seeds are smaller than our net mesh width of 200 µm. Species that do not produce seeds were also excluded: *Elodea nuttallii*, *Fallopia japonica*, *Lamiastrum galeobdolon* ssp. *argentatum* and *Petasites hybridus*. *Capsella bursa-pastoris*, *Conyza canadensis* and *Coronopus didymus* germinated in potting soil without field samples. These were also excluded to avoid possible contamination from local seed rain in the greenhouse.

Traits facilitating transport and deposition of seeds by water

Our first objective was to identify the traits that, either dependent or independent from environmental factors, may affect seed dispersal by the stream. Environmental factors considered in the water transport analyses were discharge (at the time of sampling), total amount of rainfall and average wind speed, both in 48 h preceding sampling, as possible explanatory variables. However, rainfall and wind speed were strongly related to discharge, as indicated by intracorrelation coefficients (>0.5) and variance inflation factors >2. The total amount of water that had passed the net at a given sampling day was included as an offset variable.

As traits we considered, upstream occurrence and the four functional traits release period, seed production and mass and buoyancy of seeds. Frequency was our measure of upstream occurrence. The other two, total abundance and distance, were strongly related to frequency.

To identify the key traits that facilitate seed transport and deposition by the stream, we followed the Generalised Linear Mixed Model approach of ter Braak (2019) to detect trait–environment interactions. In this approach, trait–environment interactions are entered as fixed terms, while species is included as random intercept with environment as random slope, site is included as a random intercept and trait is included as a random slope per site that is independent of the site intercepts as dependence led to convergence issues (random terms in glmmTMB code: (1 + environmental factor | Species) + (1|Site) + (0 + trait|Site)). In the context of our study, site was either considered the day of sampling (25 days in case of water transport) or each unique combination of mat and plank (30 combinations in case of water deposition). Inclusion of the random terms ‘species’ and ‘species | environment’ overcomes the problem of pseudoreplication and heteroscedastic variance (Jamil et al. 2013). Environment is either the discharge at time of sampling (in case of water transport) or elevation (in case of water deposition). Although this approach aims at detecting trait–environment interactions, it is also appropriate for testing main effects of either traits or environment (Online Resource 4).

Initially, we ran a model with all five trait–discharge or trait–elevation interactions as fixed terms. In case of nonsignificant interactions, subsequent models were run with main effects but with the same random terms. With the use of AIC, the most parsimonious model was selected.

Our analyses included all species either found in our samples or found in our field survey along the upstream stretches of the main stream and tributaries. Seeds of many species occurring upstream were not found in our samples. As a consequence, our data contained many zeroes.We therefore first tried zero-inflated models, but these did not converge. We subsequently split the analysis into analysis of presence–absence, with all species, and analysis of counts, including species with at least one seed in any of the samples. Analyses were restricted to species for which seed traits were available.

Presence–absence was analysed with a logit-link function and Bernoulli (binomial) distribution; for counts, the log-link function and the negative binomial distribution (NB2) were used. Analyses were run with glmmTMB (Brooks et al. 2017) in *R* (*R* Development Core Team 2017).

Prior to the water deposition analysis, seeds per species were summed over all samples for each combination of elevation and plank (mats). As explained above (see section 'Field study: sampling of water-deposition'), the number of sampling events differed between mats. Therefore, we included the logarithm of the number of sampling events for each mat as an offset variable.

The *R* package DHARMa (Hartig 2022) was used to check the assumptions of our models, by which several outliers were detected. Models run without these outliers did not result in qualitatively different outcomes, i.e. the same terms were significant or non-significant with or without outliers. Therefore, we present model outcomes based on the entire dataset.

Desk study: trait comparison of general and ancient forest species

Ancient and general forest species were compared for each trait that significantly explained water transport or deposition. General forest species included all species which, according to Stortelder et al. (1998), characterise *Quercus-Fraxinus-Fagus*-forests (*Quercetea* and *Querco-Fagetea)* and were not listed as ancient forest by Hermy et al. (1999). Both groups only included species occurring in the Netherlands for which trait values were available in the aforementioned databases. To emphasise, the selection of forest species was broader than species occurring in our field study area.

For each trait, a Kolmogorov Smirnov test was used to analyse whether values for ancient and general forest species represented samples from a single distribution or from two different distributions.

In case of seed production, we used the allometrical relationship between seed production per plant and maximum plant height to compare both groups, since there is a well-established relationship between both variables (Weiner et al. 2009). The height–seed production allometries were analysed with major axis regression in the 'smart' package (Warton et al. 2012). With log10-transformed seed production values, the first model tested for an interaction between log10-transformed plant height and group to address whether slopes differed between both groups. A subsequent model included only the main effects of log10 (plant height) and group, in order to test for differences in intercept between both groups (Warton et al. 2012).

Results

Field study: species and seed numbers

In the stream, a total of 17004 seeds were sampled, representing 121 species. In the upstream vegetation 247 vascular plant species were recorded. The distribution of seeds over the species was highly skewed (Fig. 1): *Alnus glutinosa*, *Lycopus europaeus* and *Urtica dioica* had about 75% of the total amount of seeds (Fig. 1).

Of the 39 ancient forest species occurring upstream, 12 were also found as seeds in the stream (Online Resource 6). Two of them, *Carex remota* and *Poa nemoralis*, were among the 20 most abundant species (Fig. 1). The ten others were: *Adoxa moschatellina*, *Anemone nemorosa, Carpinus betulus*, *Corylus avellana, Festuca gigantea, Primula elatior, Scrophularia nodosa, Stachys sylvatica, Tilia platyphyllos* and *Ulmus glabra.* There were 50 general forest species occupying upstream stretches, 15 of which were encountered as seeds in the stream water (Online Resource 6). The most abundant were *Betula spec.* and *Hederea helix* (both also included in Fig. 1).

From our deposition samples, 4014 seeds, representing 100 species, were retrieved. As in the water transport samples, *A. glutinosa* and *U.dioica* were most common. *C. remota* was the only ancient forest species among the 20 most abundant (Fig. 1). Four other ancient forest species were deposited as seed: *F. gigantea, P. nemoralis*, *S. nodosa* and *T. platyphyllos*. Eleven general forest species were found on the mats, all of them in low numbers (Online Resource 6).

Field study: trait relationships

Main effect models best fitted presence/absence of seeds and seed numbers in the stream. The probability of water transport of a seed was increased at higher discharges (Table 1). Irrespective of discharge (as there was no interaction with traits), probability was also higher for highly frequent species and for species with a long release time and high seed production. Long floating seeds also had a higher probability of dispersal, whereas heavy seeds were at a disadvantage. Similar patterns were found for seed numbers in the stream, although relations with seed production and seed mass were no longer significant. While the overall effect of seed mass

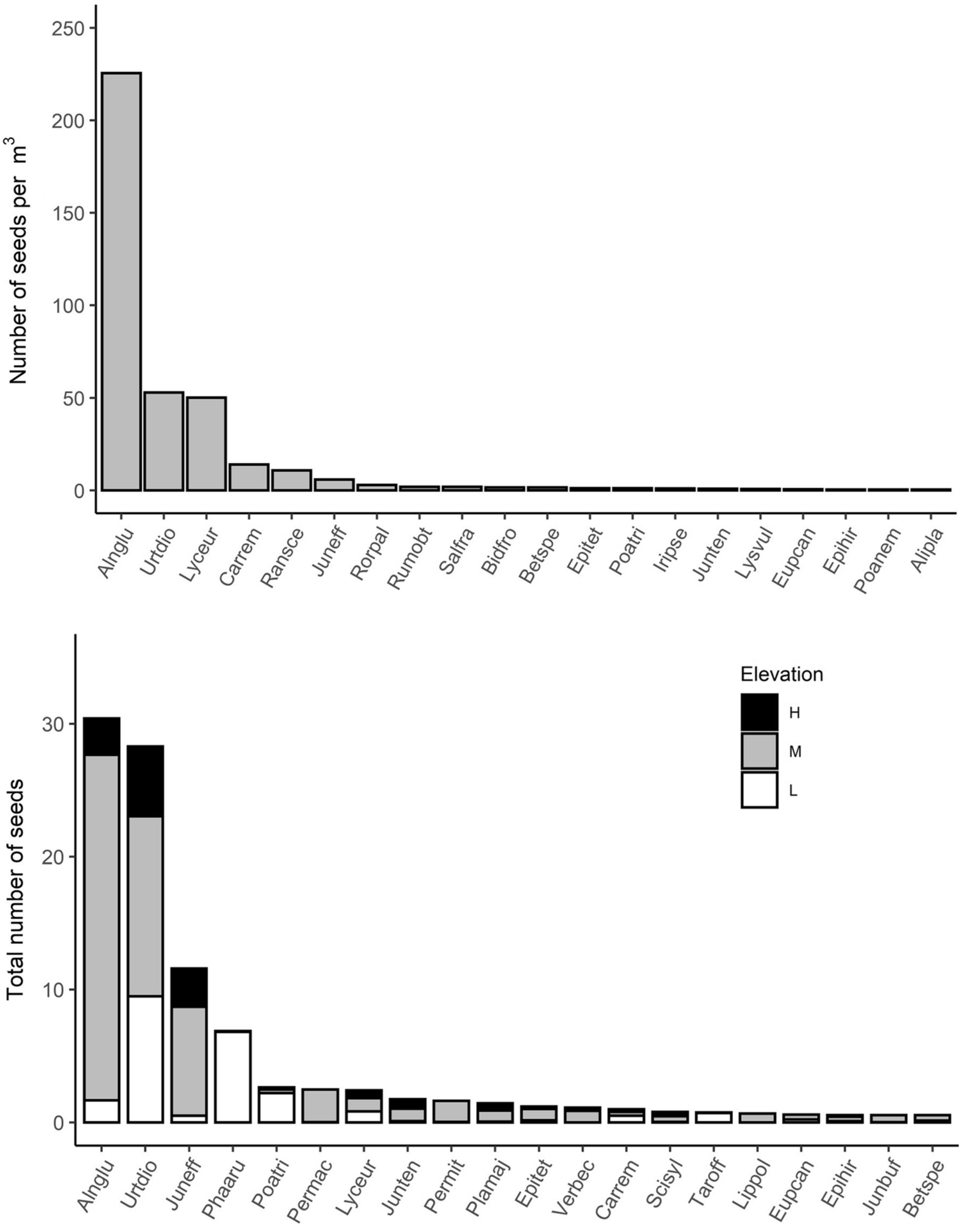

Fig. 1 Seed numbers of the 20 most abundant species in the stream samples (upper panel) and deposition samples (lower panel). Y-axis values indicate sum of seeds per m^3 of stream water (upper panel) and per mat (0.25 m^2; lower panel). Species names are indicated by first three letters of genus and species. Full names are given in Online Resource 5

on transport was negative, it differed so much across days that the effect was occasionally positive, as the coefficient of the effect is of the same order as the standard deviation.

Deposition of seeds was also best fitted by main effects models. Both with respect to probability and numbers, deposition was significantly lower at the highest elevation compared to both other elevations. Except seed production, the analysed species traits had a significant effect on seed deposition, in a similar fashion as water transport (Table 2). However, the effect of seed mass was much stronger for seed deposition than for water transport (Table 1, Table 2). This suggest that heavy seeds have an additional disadvantage when it comes to deposition by the stream on the bank.

Desk study: comparison of general and ancient forest species

As shown above, the species specific traits seed production, seed release time, buoyancy of seeds and seed mass significantly affected seed transport or deposition by the stream. Therefore, we included these traits in our subsequent desk study. Frequency was no longer included as this trait will have been specific to our studied stream.

Both groups of forest species did not differ with respect to seed release period, seed mass and seed buoyancy (Fig. 2). Seed production strongly depends on the size of the mother plant, and we therefore used an allometrical comparison between both groups (Fig. 3). Slopes of both

Table 1 Optimal models for the presence and number of seeds transported by the stream as related to species traits and discharge in the stream at the time of sampling

Random effects	Presence (logistic)	SD	Number (negative binomial)	SD
Species		2.05		1.51
Species: discharge^1		0.68		0.73
Day (of sampling)		0.52		0.64
Frequency^2: day (day)		0.16		0.12
Release period: day		0.24		0.38
Seed production^1: day		0.28		0.35
Buoyancy^3: day		0.21		0.28
Seed mass^1: day		0.61		0.52
Fixed effects	Coefficient	SE	Coefficient	SE
Intercept	−7.90	0.30***	−4.92	0.22***
Discharge^1	0.76	0.18***	0.78	0.17***
Frequency^2	1.55	0.20***	0.82	0.17***
Release period	0.47	0.18**	0.50	0.18**
Seed production^1	0.54	0.19**	0.31	0.18†
Buoyancy^3	1.10	0.21***	0.64	0.17***
Seed mass^1	−0.92	0.26***	−0.19	0.21

All variables were standardised to zero mean and unit variance to allow comparison of effect size. Table gives standard deviation for random terms and coefficients and their significance for the fixed terms of the most parsimonious general linear mixed model. The model for presence was based on a logit-link function, for seed numbers a negative binomial distribution (negbinom2) was assumed. Only species for which all analysed trait values were available were included in these analyses. The model on seed number was further restricted to species with at least one seed in any of the samples. Log values for total volume of water sampled at each date were included as offset variable. Abbreviations: SD = standard deviation; SE = standard error.

1- Log_{10}-transformed values; 2- $\text{Log}_{10}(x+0.01)$-transformed values; 3- $\text{Log}_{10}(x+1)$-transformed values. † $P<0.1$, *$P<0.05$, **$P<0.01$, ***$P<0.001$

Table 2 Main effects model for the presence and number of seeds deposited by the stream as related to species traits and elevation of sampling (high and middle relative to low)

Random effects	Presence (logistic)	SD	Number (negative binomial)	SD
Species		2.29		1.59
Species: elevation-middle		2.12		2.16
Species: elevation-high		1.99		1.74
Site		0.46		0.73
Frequency^2: site		0.25		0.23
Release period: site		0.21		0.11
Seed production: site		0.18		0.00
Buoyancy^3: site		0.26		0.15
Seed mass^1: site		0.88		0.33
Fixed effects	Coefficient	SE	Coefficient	SE
Intercept	−6.30	0.40***	−3.76	0.32***
Elevation-middle	−0.10	0.49	0.55	0.45
Elevation-high	−2.03	0.62**	−1.03	0.49*
Frequency^2	1.45	0.22***	0.72	0.18***
Release period	0.76	0.19***	0.40	0.16*
Seed production^1	0.32	0.20	0.24	0.16
Buoyancy^3	0.80	0.23***	0.45	0.16**
Seed mass^1	−1.66	0.33***	−0.56	0.19**

The term ‘site’ in the random effects part refers to all occurring combinations of elevation and plank. Log values for number of samples per site throughout the year were included as offset variable. Further notifications are according to Table 1

1- Log10-transformed values; 2- Log10(x + 0.01)-transformed values; 3- Log10(x + 1)-transformed values

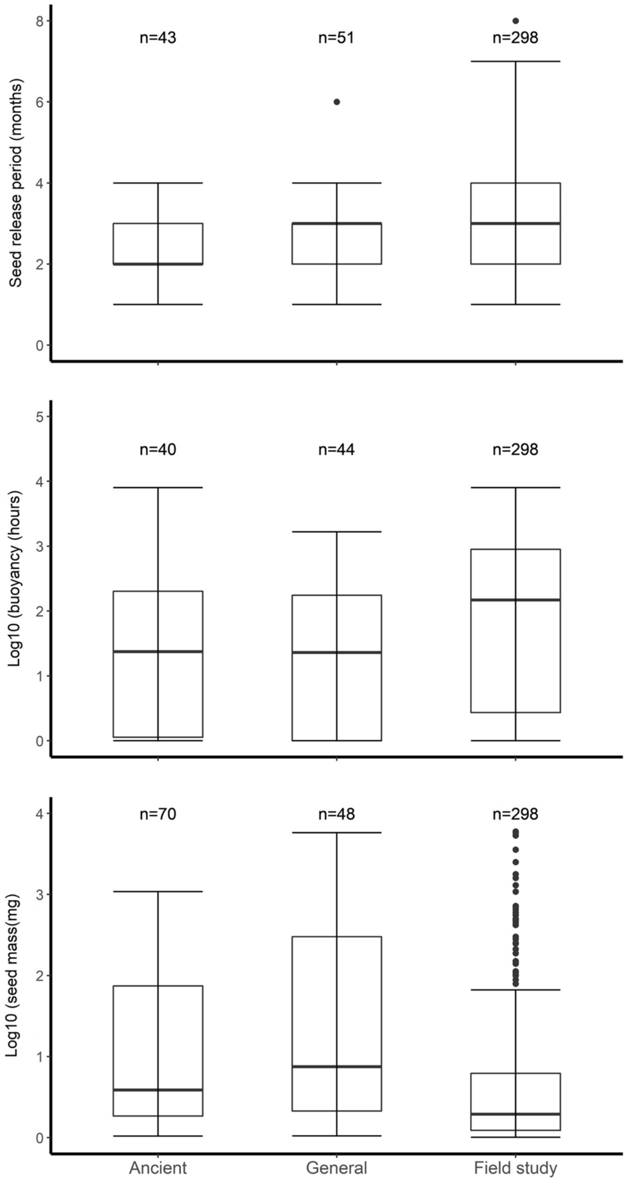

Fig. 2 Box-whiskers plots for seed release time, buoyancy and seed mass for ancient forest species ("Ancient") and general forest species ("General") as gathered in our desk study and for all species included in the field study ("Field study"). Shown are the 25, 50, and 75% quantiles and outliers (dots). Differences between both groups of forest species were analysed with a two-sample Kolmogorov Smirnov test, for none of the three indicated variables was there a significant difference between both groups. Number of species included in each group is indicated above the box-whiskers plot

groups were similar but intercept was smaller for ancient forest species, implying that, at comparable height, ancient forest species produce less seeds (Fig. 3).

Discussion

Stream dispersal of forest plants

As indicated before (Schöpke et al. 2019; von Behren and Yeakley 2020), our results show that seeds of forest plants are poorly equipped for stream dispersal compared to species from wetland or ruderal habitats (Fig. 1). Nevertheless, we observed that several forest species were transported or deposited by the stream, mostly by seed but sometimes also by vegetative diaspores (Online resource 6). In line with earlier work (Honnay et al. 2001; Araujo Calçada et al. 2013; Holeštová and Douda 2021), this shows that forest plants can be dispersed by streams. Although such dispersal events are probably rare, they may still contribute to an effective metapopulation (Verheyen et al. 2004; Soons and Ozinga 2005).

The main question of this study was whether stream dispersal mainly favours forest species common in young forest or also ancient forest species. The latter group suffers most from habitat fragmentation (van der Veken et al. 2007; Litzka and Diekmann 2019; Bergès and Dupouey 2021) as they lack adaptations for long distance dispersal by animals or wind (Hermy et al. 1999). Our comparison of both groups was based on the key traits for stream dispersal, which were first identified in a field study. As recommended by Schurr et al. (2008), we addressed both source- and path-related traits in this study.

Key traits for stream dispersal

Relevance of the source effect was indicated by significant positive terms for upstream frequency, seed production per plant and seed release period (Table 1). A likely explanation for these findings is that a larger population upstream will result in a higher amount of seeds available for seed transport downstream. Moreover, a high per plant seed production may compensate for a modest upstream population size or amplify the seed pool of large upstream populations (Boedeltje et al. 2003; van der Veken et al. 2007). Finally, seed release period may also affect the number of seeds available for transport: the longer viable diaspores are available, the higher the chance that favourable hydrological conditions occur during seed shed (Greet et al. 2012). For terrestrial plants, these favourable conditions correspond to high discharges. Larger areas bordering the stream get flooded, resulting in more seeds being picked up by the water and transported downstream (Merrit and Wohl 2002; von Behren & Yeakley 2020).

Path-related processes in our field study were mirrored by significance of stream discharge, seed buoyancy and seed mass (Table 1). More seeds were dispersed by the stream at higher discharges, but irrespective of discharge, stream

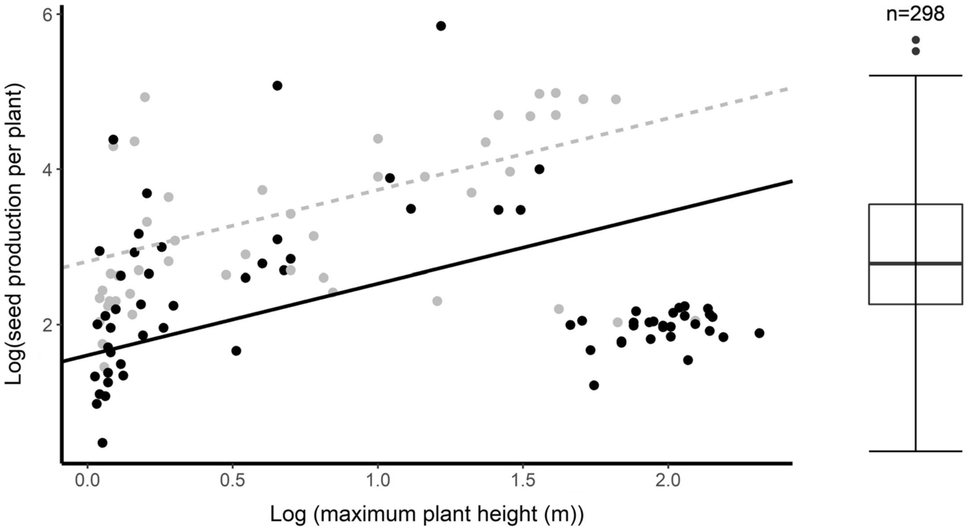

Fig.3 Log–log relationship of seed production with plant height for general (grey dots, dashed line; $n=48$) and ancient forest species (black dots and solid line; $n=70$) as gathered in our desk study. Lines represent the relationship calculated with major axis regression (sma). Sma indicated no significant difference in slopes between both forest species groups (LR statistic = 3.43, df = 1, $P=0.064$), but a significant difference in elevation between both groups (LR statistic = 28.46, df = 1, $P<0.001$). Box-whiskers plot (as in Fig. 2) shows the variation of all the species included in our field study

dispersal was more frequent for long-floating and light seeds. Floating capacity enables transport on the surface of the water which will allow downstream dispersal at low flow velocities (Boedeltje et al. 2003), whereas at raised water levels, floating seeds may easily be lifted over barriers such as emergent vegetation or woody debris (Nilsson et al. 2010; von Behren & Yeakley 2020).

Due to the flowing water, streams may also transport non-floating seeds. This may happen if seeds are suspended in the water column or rolling over the streambed. The lighter the seeds the more likely these mechanisms are likely to operate (Nilsson et al. 2010; Carthey et al. 2016). This explains why, in addition to seed buoyancy, seed mass also emerged as an important trait explaining water transport.

Our analyses of seed deposition (Table 2) indicated that high seed mass may also hamper deposition on the riparian zone. This finding corroborates the study by Gurnell et al. (2008) who found that seeds of species being deposited by streams were lighter than those of species present in the stream bed. In line with Fraaije et al. (2017), we found decreased seed deposition at the highest elevation, suggesting that more frequently flooded sites trap more seeds. Such sites are also prone to frequently receding water levels, which are necessary for entrapment of seeds in vegetation and sedimentation of suspended seeds (Merritt and Wohl 2002).

Hydrochorous capacity of young and ancient forest species

Having identified the key traits for stream dispersal in a field study, we subsequently performed a desk study to test whether these key traits differ among ancient forest and general forest species. This step included more forest species than collected in the field study since seeds of both species groups were rare in our field samples thus hampering a direct comparison. We feel confident about our approach since the range encompassed by both groups of forest species fell within the range of key traits identified in our field study (Figs.2, 3).

The trait comparison of both groups only revealed a consistent difference with respect to seed production, at a given plant height seed production of ancient forest species was less (Fig. 3). This life history trait is a well-known adaptation to low-disturbance environments such as ancient forests. In these environments, investments in adult longevity are more adaptive (Verheyen et al. 2003; Adler et al. 2013), but our study has indicated that such an adaptation may come at the expense of long distance stream dispersal.

Conclusion

Our results confirm earlier findings (Honnay et al. 2001; Araujo Calçada et al. 2013; Holeštová and Douda 2021) that streams may contribute to long distance dispersal of ancient forest plants and thus accelerate their establishment in young forests. This is based on our finding that seeds of ancient forest do not consistently differ from other forest species with respect to stream dispersal capacity. However, the extent of stream dispersal will critically depend on upstream population size, given the relatively low per plant seed production of ancient forest species. Moreover, our results indicate that stream dispersal will not work for all forest species. Particularly species with heavy seeds will hardly be replaced by the stream, let alone be deposited in suitable forest patches downstream.

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Author contributions GB designed the research, collected and processed samples, identified plant diaspores and performed additional buoyancy measurements. GB and JL surveyed the upstream vegetation, analysed data (with support of CtB and BvZ) and wrote the manuscript. To our deep regret, Ger Boedeltje passed away before the manuscript was finished.

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Declarations

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References

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M (2013) Functional traits explain variation in plant life history strategies. PNAS 111:740–745. https://doi.org/10.1073/pnas.1315179111

Araujo Calçada E, Closset-Kopp D, Gallet-Moron E, Lenoir J, Rêve M, Hermy M, Decocq G (2013) Streams are efficient corridors for plant species in forest communities. J Appl Ecol 50:1152–1160. https://doi.org/10.1111/1365-2664.12132

Baeten L, Hermy M, Verheyen K (2009) Environmental limitation contributes to the differential colonization capacity of two forest herbs. J Veg Sci 20:209–223. https://doi.org/10.1111/j.1654-1103.2009.05595.x

Baeten L, Velghe D, Vanhellemont M, De Frenne P, Hermy M, Verheyen K (2010) Early trajectories of spontaneous vegetation recovery after intensive agricultural land use. Restor Ecol 18:379–386. https://doi.org/10.1111/j.1526-100X.2009.00627.x

Baskin CC, Baskin JM (2014) Seeds, Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego

Bergès L, Dupouey J-L (2021) Historical ecology and ancient forests: progress, conservation issues and scientific prospects, with some examples from the French case. J Veg Sci 32(1):e12846

Boedeltje G, Bakker JP, Bekker RM, Van Groenendael JM, Soesbergen M (2003) Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. J Ecol 91(5):855–866. https://doi.org/10.1046/j.1365-2745.2003.00820.x

Boedeltje G, Bakker JP, ten Brinke A, van Groenendael JM, Soesbergen M (2004) Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. J Ecol 92:786–796. https://doi.org/10.1111/j.0022-0477.2004.00906.x

Bossuyt B, Hermy M, Deckers J (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. J Ecol 87:628–638. https://doi.org/10.1046/j.1365-2745.1999.00379.x

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. R J 9:378–400

Brudvig LA, Mabry CM, Mottl LM (2011) Dispersal, not understory light competition, limits restoration of Iowa woodland understory herbs. Restor Ecol 19:24–31. https://doi.org/10.1111/j.1526-100X.2010.00675.x

Brunet J, von Oheimb G (1998) Migration of vascular plants to secondary woodlands in southern Sweden. J Ecol 86:429–438. https://doi.org/10.1046/j.1365-2745.1998.00269.x

Brunet J, De Frenne P, Holmström E, Lajos Mayra M (2012) Life-history traits explain rapid colonization of young post-agricultural forests by understory herbs. Forest Ecol Manag 278:55–62. https://doi.org/10.1016/j.foreco.2012.05.002

Carthey AJR, Fryirs KA, Ralph TJ, Bu H, Leishman M (2016) How seed traits predict floating times: a biophysical process model for hydrochorous seed transport behaviour in fluvial systems. Freshw Biol 61:19–31. https://doi.org/10.1111/fwb.12672

Development Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna

Duistermaat L (2020) Heukels' Flora van Nederland, 24th edn. Naturalis Biodiversity Center/Wolters-Noordhoff, Groningen, Netherlands

Fraaije RGA, Moinier S, van Gogh I, Timmers R, van Deelen JJ, Verhoeven JTA, Soons M (2017) Spatial patterns of water-dispersed seed deposition along stream riparian gradients. PLoS ONE 12(9):e0185247. https://doi.org/10.1371/journal.pone.0185247

Greet J, Cousens RD, Webb JA (2012) Flow regulation affects temporal patterns of riverine plant seed dispersal: potential implications for plant recruitment. Freshw Biol 57:2568–2579. https://doi.org/10.1111/fwb.12028

Grime JP, Hodgson JG, Hunt R (1989) Comparative Plant Ecology. A functional approach to common British species, Unwin Hyman, London

Gurnell A, Thompson K, Goodson J, Moggridge H (2008) Propagule deposition along river margins: linking hydrology and ecology. J Ecol 96:553–565. https://doi.org/10.1111/j.1365-2745.2008.01358.x

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. **R** package version 0.4.5. https://CRAN.R-project.org/package=DHARMa

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol Conserv 91:9–22. https://doi.org/10.1016/S0006-3207(99)00045-2

Hintze C, Heydel F, Hoppe C, Cunze S, König A, Tackenberg O (2013) D3: the dispersal and diaspore database–Baseline data and statistics on seed dispersal. Perspect Plant Ecol Ev 15:180–192. https://doi.org/10.1016/j.ppees.2013.02.001

Holeštová A, Douda J (2021) Plant species over-occupancy indicates river valleys are natural corridors for migration. Plant Ecol 223:71–83. https://doi.org/10.1007/s11258-021-01191-9

Honnay O, Hermy M, Coppin P (1999) Impact of habitat quality on forest plant species colonization. Forest Ecol Manag 115:157–170. https://doi.org/10.1016/S0378-1127(98)00396-X

Honnay O, Verhaeghe W, Hermy M (2001) Plant community assembly along dendritic networks of small forest streams. Ecol 82:1691–1702. https://doi.org/10.1890/0012-9658(2001)082[1691:PCAADN]2.0.CO;2

Jamil T, Ozinga WA, Kleyer M, ter Braak CJF (2013) Selecting traits that explain species-environment relationships: a generalized linear mixed model approach. J Veg Sci 24:988–1000. https://doi.org/10.1111/j.1654-1103.2012.12036.x

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M et al (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Kondo T, Miura T, Okubo N, Shimada M, Baskin C, Baskin J (2004) Ecophysiology of deep simple epicotyl morphophysiological dormancy in seeds of *Gagea lutea* (*Liliaceae*). Seed Sci Res 14:371–378. https://doi.org/10.1079/SSR2004182

Litza K, Diekmann M (2019) Hedgerow age affects the species richness of herbaceous forest plants. J Veg Sci 30:553–563. https://doi.org/10.1111/jvs.12744

Merritt DM, Wohl EE (2002) Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. Ecol Appl 12:1071–1087. https://doi.org/10.1890/1051-0761(2002)012[1071:PGHARH]2.0.CO;2

Naaf T, Kolk J (2015) Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. Biol Cons 183:155–163. https://doi.org/10.1016/j.biocon.2014.12.002

Newton RJ, Hay FR, Ellis RH (2015) Ecophysiology of seed dormancy and the control of germination in early spring-flowering *Galanthus nivalis* and *Narcissus pseudonarcissus* (*Amaryllidaceae*). Bot J Linn Soc 177:246–262. https://doi.org/10.1111/boj.12240

Nilsson C, Brown RL, Jansson R, Merritt DM (2010) The role of hydrochory in structuring riparian and wetland vegetation. Biol Rev 85:837–858. https://doi.org/10.1111/j.1469-185X.2010.00129.x

Peterken GF (1974) A method for assessing woodland flora for conservation using indicator species. Biol Conserv 6(4):239–245. https://doi.org/10.1016/0006-3207(74)90001-9R

Schöpke B, Heinze J, Pätzig M, Heinken T (2019) Do dispersal traits of wetland plant species explain tolerance against isolation effects in naturally fragmented habitats? Plant Ecol 220:801–815. https://doi.org/10.1007/s11258-019-00955-8

Schurr FM, Steinitz O, Nathan R (2008) Plant fecundity and seed dispersal in heterogenous environments: models, mechanisms and estimation. J Ecol 96:628–641. https://doi.org/10.1111/j.1365-2745.2008.01371.x

Silvertown JW, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63. https://doi.org/10.1038/21877

Soons MB, Ozinga WA (2005) How important is long-distance seed dispersal for the regional survival of plant species? Divers Distrib 11:165–172. https://doi.org/10.1111/j.1366-9516.2005.00148.x

Stortelder AHF, Schaminée JHJ, Hommel PWFM, Westhoff V (1998) De Vegetatie van Nederland Deel5 Plantengemeenschappen van ruigten, struwelen en bossen. Opulus Press, Uppsala, Leiden

ter Braak CJF (2019) New robust weighted averaging- and model-based methods for assessing trait–environment relationships. Methods Ecol Evol 10:1962–1971. https://doi.org/10.1111/2041-210X.13278

van der Veken S, Bellemare J, Verheyen K, Hermy M (2007) Life history traits are correlated with geographic distribution patterns of Western European forest plants. J Biogeogr 34:1723–1735. https://doi.org/10.1111/j.1365-2699.2007.01738.x

Verheyen K, Hermy M (2001) The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. J Ecol 89:829–840. https://doi.org/10.1046/j.0022-0477.2001.00596.x

Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003) Response of forest plant species to land-use change: a life-history trait-based approach. J Ecol 91:563–577. https://doi.org/10.1046/j.1365-2745.2003.00789.x

Verheyen K, Vellend M, van Calster H, Peterken G, Hermy M (2004) Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. Ecol 85:3302–3312. https://doi.org/10.1890/04-0395

von Behren C, Yeakley JA (2020) Hydrochorous seed dispersal in riparian forests altered by urbanization. Ecosphere 11(2):e03049. https://doi.org/10.1002/ecs2.3049

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) Smatr 3–An R package for estimation and inference about allometric lines. Methods Ecol Evol 3:257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Weiner J, Campbell LG, Pino J, Echarte L (2009) The allometry of reproduction within plant populations. J Ecol 97:1220–1232. https://doi.org/10.1111/j.1365-2745.2009.01559.x