Directed dispersal by an abiotic vector: wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water

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Summary

1. Plant species around the world invest in seed dispersal by producing large numbers of seeds, with a wide range of morphological adaptations that facilitate dispersal. Not all dispersed seeds reach suitable sites, however, and plants can significantly improve their fitness by increasing the proportion of seeds arriving at suitable sites for germination and establishment. Disproportionate dispersal to suitable sites is known as 'directed dispersal'. Yet, mechanisms of directed dispersal are only known for a limited number of animal-dispersed plant species.

2. We tested the hypothesis that directed dispersal can also be driven by abiotic vectors, such as water or wind. We used a tiered approach, combining analyses of experimental, field and literature data on wetland plant species and evaluating the potential for evolution of directed dispersal with a spatially explicit individual-based model.

3. The data collected demonstrate that wetland plants produce seeds with adaptations to promote transportation and deposition by water towards microsites along the hydrological gradient where they germinate and establish best. Aquatic species produce seeds that sink and are transported by water as bed load towards inundated sites. In contrast, shoreline species produce seeds that float for very long periods of time so that they are eventually entrapped by shoreline vegetation or deposited at the waterline. Our model simulations confirm that the patterns we observed in nature can evolve under natural selection through adaptations in seed buoyancy.

4. For wind dispersal, the situation is more complex. Wind does not provide directed dispersal in the strictest sense but, rather, simply appears to be the best available dispersal vector for more terrestrial wetland plant species to reach drier areas in a wet environment.

5. *Synthesis*. We show that directed dispersal towards specific, suitable microsites is not exclusive to animal-dispersed plant species, but may be far more common in plants – also in species dispersed by abiotic vectors, in particular water. As water and wind are very common dispersal vectors throughout the plant kingdom, directed dispersal (and not just dispersal distance) seems to be of general importance for the ecology of plants.

Key-words: anemochory, biodiversity, evolutionary adaptations, hydrochory, hydrological niche, plant functional traits, riparian zones, seed dispersal, water dispersal, wind dispersal

Introduction

In sessile organisms such as plants, the dispersal of propagules away from the parent is essential for maintaining species survival and diversity (Levin *et al.* 2003). Dispersal creates spatial structure within populations (Nathan & Muller-Landau 2000) and preserves spatial population dynamics, gene flow and regional species survival (Ozinga *et al.* 2009; Lesser & Jackson 2013; Mari *et al.* 2014). It also enables colonization of new areas,

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including restored sites and new habitat ranges following climate change (Honnay *et al.* 2002; Brederveld *et al.* 2011; Nathan *et al.* 2011). In flowering plants, seeds or fruits (hereafter referred to collectively as 'seeds') are typically the units that disperse (Van der Pijl 1982). The study of seed dispersal mechanisms receives much attention, but important aspects including the adaptive nature of dispersal are still poorly understood (Holyoak *et al.* 2008; Nathan *et al.* 2008; Buoro & Carlson 2014).

Plant species around the world produce seeds in large numbers and with a wide range of morphological adaptations to facilitate dispersal (Van der Pijl 1982). These investments imply that major fitness benefits can be gained via seed dispersal (Howe & Smallwood 1982; Levin & Muller-Landau 2000; Levin *et al.* 2003). Not all dispersed seeds reach sites suitable for germination and establishment, however, and plants can significantly improve their fitness by increasing the proportion of seeds that are dispersed to 'suitable sites' – *that is* sites with a predictably high probability of germination and establishment. Such disproportionate dispersal to suitable sites is known as 'directed dispersal' (Howe & Smallwood 1982; Wenny 2001).

To date, directed dispersal has almost exclusively been observed in animal-dispersed plant species (e.g. Wenny & Levey 1998; Spiegel & Nathan 2007; Briggs, Wall & Jenkins 2009; Carlo *et al.* 2013): of the 110 data papers referring to 'directed dispersal' since 1988 (ISI Web of Knowledge, 15 July 2015), 106 address dispersal by animals (mostly birds, ants and scatter-hoarding rodents). The rapid increase in research in this area (68 of the 110 papers appeared in the past 5 years) is a testament to the growing interest in this topic – but the focus on animal-mediated dispersal remains unchanged. Yet, from an evolutionary perspective, it would make sense that directed dispersal is a more widespread phenomenon, existing also in plant species dispersed by other vectors. Water and wind are very common dispersal vectors in plants (Van der Pijl 1982), and if they also mediate directed dispersal, this process plays a far more important role in ecology than currently recognized.

Flume experiments suggest that water flow has the potential to deposit seeds at specific microsites (Merritt & Wohl 2002). Species-specific differences in seed arrival patterns following water or wind dispersal have been suggested or observed under natural conditions in forest gaps and across stream riparian zones (Augspurger & Franson 1988; Nathan *et al.* 2005; Fraaije *et al.* 2015b). However, ecological adaptations to directed dispersal by water or wind and underlying mechanisms have been proposed in only very few cases (gap colonizing tree species, Nathan *et al.* 2005; riparian willows, Seiwa *et al.* 2008; rainfall-dispersed alpine *Veronica*, Pufal & Garnock-Jones 2010). The existence of directed dispersal by water or wind, and its potential ecological importance, has therefore remained speculative.

The combination of parental investment in morphological adaptations to facilitate seed dispersal and

species-specific seed arrival patterns observed in the field leads us to hypothesize that directed dispersal also exists in species dispersed by abiotic vectors. We therefore investigated whether directed dispersal exists in plant species dispersed by water and wind. Riparian and littoral wetlands cover the water–land interface of streams, rivers and shallow lakes. They represent highly interconnected, dynamic habitats with a strong hydrological gradient that supports a wide range of plants species each occupying a relatively narrow hydrological niche (Naiman & Décamps 1997; Silvertown *et al.* 1999; Silvertown, Araya & Gowing 2015). Such systems provide ideal conditions to test whether wetland plant species possess morphological adaptations that facilitate directed dispersal by water or wind towards their hydrological niche. We collected and analysed experimental data on representative wetland plant species and analysed field data and trait distributions across wetland species from the literature. We then evaluated the potential for evolution of directed dispersal in wetland species using a theoretical modelling framework. Our results consistently provide support for directed dispersal by water, showing that directed dispersal by abiotic vectors is possible and even likely to be common. This suggests a far wider importance of directed dispersal in plant ecology than previously supposed.

Materials and methods

To investigate whether wetland plant species have morphological adaptations facilitating directed dispersal by water or wind, we used a tiered approach. First, we quantified seed dispersal and germination traits of a representative set of species under controlled conditions in the greenhouse. Secondly, we analysed field data on seed arrival and germination patterns of many species under a range of natural conditions. Thirdly, we examined species' trait data from the literature to evaluate patterns across a wide range of species and communities. Specifically, we used the experimental data to evaluate whether (i) species with different hydrological niches have seeds with morphological adaptations that promote differential dispersal by water and/or wind, (ii) this would result in differential seed transport and deposition mechanisms across the hydrological gradient, and (iii) the specific hydrological microsites where these seeds would arrive are optimal for their germination. We used the field data to evaluate whether (iv) species with different hydrological niches produce seeds that arrive at different positions along the hydrological gradient, and whether (v) these positions are suitable for germination and establishment. We used the literature data to evaluate the evidence for these patterns across a wide range of wetland species as possible. Finally, we evaluated the potential for evolution of directed dispersal in wetland species using a spatially explicit individual-based model.

EXPERIMENTAL DATA COLLECTION

We selected 23 plant species that are common in North-West Europe and representative for plants from a wide range of habitats: from the open water in lakes, streams and ditches, to their shorelines, to increasingly terrestrial wetland areas (table S1 in Appendix S1, Supporting Information). In their natural habitat, these species have two common abiotic dispersal vectors at their immediate disposal: water and wind. We quantified each species' niche along the hydrological gradient as the average water level at

which the species occurs (where positive water levels indicate submerged conditions, water levels around zero indicate the shoreline, and increasingly negative water levels indicate increasingly dry conditions). Average water levels were calculated from the range of water levels sampled in five natural populations per species, in the Netherlands.

To investigate whether species with different hydrological niches have seeds with morphological adaptations that promote differential dispersal by water and wind, we quantified their seed morphology (density, mass, diameter), floating capacity (buoyancy, in FP50 – the time it takes for 50% of seeds to sink; cf. Boedeltje *et al.* 2003; Van den Broek, Van Diggelen & Bobbink 2005) and terminal velocity (the constant falling rate in still air, in m/s; cf. Soons & Heil 2002; Soons *et al.* 2004). We measured these on sets of 20 randomly selected individual seeds, collected from three natural populations, per species.

As differential dispersal abilities by water and wind would result in differential seed arrival across the hydrological gradient, we investigated if the hydrological microsites of expected arrival are suitable for germination. To this purpose, we carried out a seed germination experiment with different hydrological conditions. After a stratification period, we placed 20 randomly selected seeds per species in the greenhouse on sterilized river sand under four different conditions: water level 40 cm above soil level (inundated treatment), water level equal to soil level (waterlogged treatment), water level 4 cm below soil level (field capacity treatment) and water level 6·5 cm below soil level (dry treatment). All treatments were replicated three times. Greenhouse conditions were set to optimize seed germination, at light/dark 16/8 h and 24°/12 °C.

Full details on the experimental conditions and measurements are given in Appendix S2.

FIELD DATA COLLECTION

We monitored natural seed deposition and germination along the riparian gradients of three sandy-substrate lowland streams in the Netherlands: the Hagmolenbeek (HM), Hooge Raam (HR) and Kleine Aa (KA). We monitored seed deposition in the first year following restoration of each stream. Restoration activities included removal of all existing vegetation and excavation of the riparian zone to re-create natural, gradually levelling, v-shaped stream valleys. This allowed us to quantify natural seed dispersal by water and wind without interference by local seed rain (i.e. seeds falling directly from the plant without being dispersed).

In each stream, we monitored seed deposition using three replicate transects. Each transect consisted of five seed traps (25 × 25 cm Astroturf mats, with 1·5 cm bristles and ca. 8 bristles per cm^2), pinned to the ground along the riparian hydrological gradient perpendicular to the stream at a distance of approximately 0·5, 1·0, 3·0 and 5·0 m from each other, spanning the entire gradient from permanently inundated to permanently dry. Each seed trap was removed after 6 months and replaced by a clean mat. Seed trap contents were processed and analysed for total number of viable seeds per species following Fraaije *et al.* (2015b). For each trap, the average water level (as defined above) was calculated for the half year it was out in the field, using stream water levels registered hourly with pressure transducers (Schlumberger Water Services, Delft, the Netherlands; Keller Meettechniek B.V., Reeuwijk, the Netherlands) in water level gauges. In our data analysis on trapped seeds, we excluded seeds of a very few species that had not been removed entirely by the restoration activities, or had established in the first months after restoration, to exclude local seed rain.

During spring and summer (May to August), a field germination trial was performed next to each seed trap. We introduced seeds of 17 typical riparian plant species that are common across the research area (Table S3). Again, plant species were selected to be representative for the entire range of hydrological conditions along the riparian gradient. Seeds were purchased from commercial suppliers which collect seeds from natural wild populations. All seeds were stratified and then introduced to the field sites in two sets of mesh bags (mesh size 680 μm, thread diameter 150 μm) which contained 20 seeds per species per bag and were pinned to the sediment in each plot. After 2 and 3 months (to evaluate possible effects of environmental fluctuations over time), the mesh bags were removed to score germination as per Fraaije *et al.* (2015a). Germination during the two periods was pooled for further analysis.

Full details on the field sites are given in Fraaije *et al.* (2015a,b).

LITERATURE DATA COLLECTION

We did not attempt meta-analysis of existing data on directed dispersal by abiotic vectors, as we found only five data papers in the literature that address directed dispersal in relation to wind or water. Instead, we investigated the evidence for adaptations for directed dispersal across wetland communities, by analysing data available on species traits and hydrological niches for as wide a range of wetland species as possible. To this purpose, we combined existing data as accumulated in two large data bases.

The PLANTATT data base (Hill, Preston & Roy 2004; excerpt 5 December 2006) reports Ellenberg values updated for all British and Irish plants and is therefore representative for Atlantic North-Western Europe. From this data base, we extracted Ellenberg F indicator values for habitat moisture ('*Feuchtigkeit*'), which indicate the optimal habitat of plant species along the full range of existing habitat moisture conditions on an ordinal scale from 1 to 12 (Ellenberg *et al.* 1991; Hill *et al.* 1999). We used these Ellenberg F-values to approximate the niche of species along the hydrological gradient. The LEDA traitbase (Kleyer *et al.* 2008; excerpt 13 July 2010) reports life history traits of the Northwest European flora. From this, we extracted seed buoyancy and terminal velocity data. In this data base, buoyancy is quantified as percentage of seeds still floating 1 week after immersion in water. For all species occurring in wetlands (according to Schaminée *et al.* 1999) for which Ellenberg F-values and buoyancy or terminal velocity data were available, we analysed the distribution of the trait values across the niches.

STATISTICAL ANALYSIS

We analysed relations between plant and seed traits using Linear Models (lm) in R (version 3.0.1; The R Foundation for Statistical Computing). We tested whether plant and seed traits were related either linearly (using the linear function) or unimodally (using the simplest, quadratic function). When both functions gave significant fits to the data, we compared the fits using the small-sample version of Akaike Information Criterion (AICc, calculated using the AICcmodavg package in R), which performs better for small N but converges to AIC for large N (Burnham & Anderson 2004). When the difference between both fits was relatively small (dAICc < 5·5), we selected the linear model as best (simplest) function. When dAICc was 'considerable' (>5·5; Burnham & Anderson 2004), we selected the model with the lowest AICc. More flexible unimodal functions (particularly, functions allowing asymmetry) would obviously fit the data better, but our main point here was not to find the function that best fitted the data but to assess the general shape and significance of the relations.

THEORETICAL MODELLING FRAMEWORK

We simulated evolution of traits promoting differential seed dispersal by wind and water, through natural selection on seed

buoyancy and terminal velocity, in relation to species hydrological niches. We did this using a simple spatially explicit individual-based model. The environment was modelled as a rectangular lattice of 50 by 500 (X by Y) cells, with reflective boundaries for X and toroidal for Y. Each cell could contain a single plant individual. A stream flowed along the Y-axis of the lattice, with a total width of 20 cells ($-10 < X < 10$).

At the start of the simulation, individuals were introduced into the environment, each assigned a random location, buoyancy, terminal velocity and hydrological niche. Locations were drawn as rounded random X- and Y-coordinates from the lattice ($0 < X < 50$; $0 < Y < 500$). Buoyancy (B; defined as the number of time steps within a plant generation that a seed can remain afloat) was drawn randomly from a uniform distribution ($0 \leq B \leq 30$ time units). As a measure of terminal velocity, we randomly assigned a parameter for wind dispersal distance to each individual ($0 > D > 10$ cells), which specifies the variance of the Gaussian distribution from which dispersal distances are drawn. Hydrological niche (defined as the range of X-coordinates, representing the moisture gradient, where the individual would survive) was drawn randomly from a uniform distribution ($0 \leq H \leq 50$). For each individual, the hydrological niche was calculated as $0.6H \leq X \leq 1.4H$. In this way, niche breadth increases with distance from the stream, simulating a natural, gradually levelling, v-shaped riparian zone.

The model was initialized with a first batch of 25 000 random individuals, of which only those located within their hydrological niche survived (ca. 16 000 individuals). Because each cell could hold only one individual, at each time step a random survivor was chosen from those individuals that had been assigned the same location and were within their hydrological niche. In this way, we explored the potential for selection for directed dispersal (individuals whose seeds are more successful in arriving within their hydrological niche have an advantage over others) while taking into account selection for dispersal (individuals whose seeds disperse farther away from the parent arrive with lower numbers of siblings per cell and thus avoid sibling competition, which gives them an advantage over others as long as the arrival sites are suitable). Each surviving plant generated 10 seeds, with the same B, D and H as the parent individual and a mutation rate $m = 0.0001$. For simplicity, we considered asexual reproduction and non-overlapping generations.

For each generation, seeds were dispersed via wind within the first time step and subsequently through water in the next 30 time steps. All seeds were wind-dispersed in a random direction according to their wind dispersal capacity D. Seeds with $B > 0$ and located in the water column moved with the flow 1 cell down along the Y-axis and randomly 0, 1 or -1 cells in the X-direction. The waterline (WL; defined as the absolute value of the X-coordinates below which cells are in the stream and above which cells are on the stream bank) was set to fluctuate using a sinusoid, a cosine wave and some normally distributed randomness, resulting in a curve that resembles natural water level fluctuations that vary stochastically over time:

$$\text{WL} = \text{WL}_{t=0} + 2 \cdot \sin(2t) + \cos(100t) + \varepsilon,$$

where t is the time step and ε is an error term drawn from a Gaussian distribution with $\mu = 0$ and $\sigma = 2$. When the water receded, seeds were deposited on the stream bank when $|X_i| > $ WL; in contrast, a rising water level could detach seeds from their location if $B_i > t$. Seeds with $B_i < t$ located in the permanently aquatic part of the stream ($-0.25 \cdot$ mean WL $< X < 0.25 \cdot$ mean WL) dispersed by rolling over the bottom 1 cell per time step in the Y-direction and randomly left or right in the X-direction. All redistribution of seeds was terminated after 30 time steps, when only those individuals located within their hydrological niche were selected to compete for space. When multiple selected seeds ended in the same cell, a random individual was chosen to contribute offspring to the

next generation. We simulated 500 generations according to these simple rules and reported the trait combinations (HxB) and (HxD) present in the 500th generation. To report H consistently with the average water levels defined above, we rescaled them as follows: standardized hydrological niche $H' = (\text{meanWL-}H)/\max(H\text{-meanWL})$. We performed model sensitivity analyses to evaluate the sensitivity of simulation results to the model settings (i) initial population size, (ii) number of generations, (iii) increasing niche breadth with distance to the stream, and (iv) stream width (Appendix S7). Model simulations were performed in MATLAB (R2014b; The Mathworks, Inc.).

Results

EXPERIMENTAL DATA

The 23 plant species each have a well-defined, species-specific hydrological niche across the investigated wetlands (Fig. 1a, table S1 in Appendix S1). Together, they represent the range from submerged growth in open water (down to ca. 1.5 m deep) to terrestrial wetland habitat (up to >0.5 m above water).

The dispersal abilities of the plant species varied with their niche along the hydrological gradient. The relationship between water dispersal ability (as measured by buoyancy) and hydrological niche was unimodal (Fig. 1b; Table S4, $R^2 = 0.32$, d.f. = 21, $P = 0.008$, $Y = 6.2 + 0.9X – 9.8X^2$). Seeds of plants from the wettest, inundated, niches sank to the bottom after very short time intervals. This indicates that in the field, their dispersal would be limited to transport as bed load towards aquatic, inundated sites within the water body. Seeds of shoreline plants floated for long, almost unlimited, periods of time. Simple rules of physics suggest that such long floating times ensure entrapment of seeds in the shoreline vegetation or deposition at the waterline. Seeds of plants from higher elevations along the hydrological gradient had a range of intermediate buoyancies, indicating intermediate abilities for dispersal by water. In contrast, wind dispersal ability (as measured by the inverse of terminal velocity) was almost absent in plants growing under very wet conditions and increased linearly with niche distance above the water level (Fig. 1c; Table S4, $R^2 = 0.40$, d.f. = 20, $P = 0.001$, $Y = 1.6 + 1.9X$).

Plant trait measurements suggest that these dispersal abilities are at least partly explained by morphological seed traits. Water dispersal ability was correlated with seed density in most species (Fig. S5a; Table S4). Particularly, seeds with densities >1 mg mm^{-3} (the density of water) had relatively short floating times. Wind dispersal ability was strongly correlated with the ratio of the square root of the seed mass to the seed diameter (Fig. S5b; Table S4).

Results of the seed germination experiment showed that the optimal hydrological conditions for germination correlated strongly and linearly with the hydrological niches of the species (Fig. 1d; Table S4, $R^2 = 0.34$, d.f. = 19, $P = 0.003$, $Y = 2.4 – 1.4X$). Seeds of the species from inundated niches germinated best underwater and seeds from species of increasingly dry niches germinated best under increasingly dry conditions.
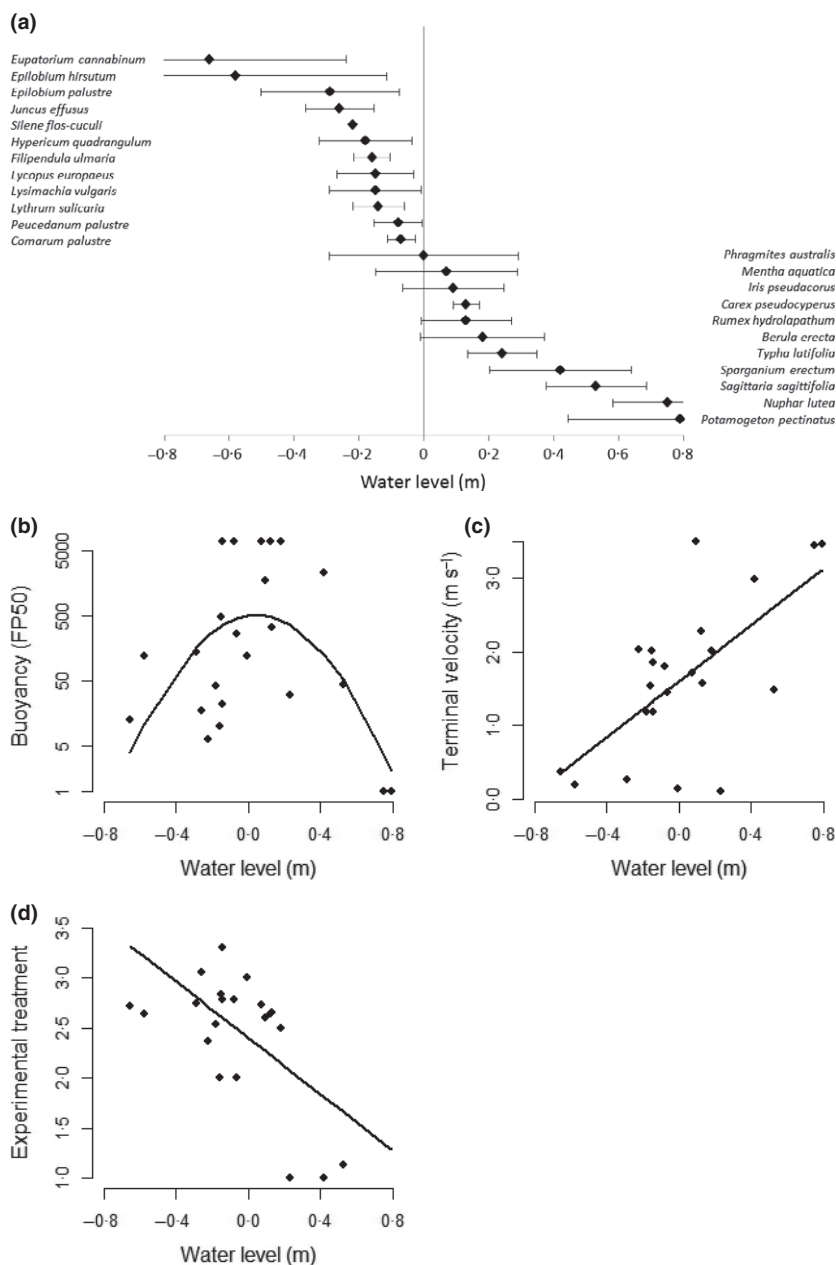
Fig. 1. (a) The 23 wetland species investigated in this study each have a species-specific niche along the hydrological gradient in the wetlands where they occur (means and standard deviations indicated). Positive water levels indicate inundated sites, and negative water levels indicate sites above the surface water level. (b) The species have differential abilities for dispersal by water, as indicated by seed buoyancy (expressed as time until 50% of seeds have sunk, FP50; zero values on log scale plotted as unit values). (c) The species have differential abilities for dispersal by wind, as indicated by seed terminal velocity. (d) Hydrological conditions required for germination are related to the hydrological niche of the species. The *y*-axis reports weighted averages of seeds germinating in the germination trials, using ordinal values, with '1' indicating inundated, '2' waterlogged, '3' field capacity and '4' dry conditions.

FIELD DATA

The arrival of seeds along the hydrological gradients of the restored streams was not random. Analysis of all trapped seeds showed that there was a positive linear relation between community-weighted average Ellenberg F-values of the trapped seeds per mat and water level (Fig. 2a; $R^2 = 0.33$, d.f. = 38, $P < 0.001$, $Y = -1.8 + 0.2X$). This indicates that seeds of aquatic plants arrived in relatively greater numbers at the wetter, inundated end of the investigated gradient and species from increasingly dry niches arrived in relatively greater numbers at increasingly dry sites. Analysis of the data per site and sampling period showed that the arrival of seeds along the hydrological gradient was positively and linearly related to species' hydrological niches as expressed by their Ellenberg F-values, for almost all sampled sites and periods (Fig. S6).

In addition to differential arrival, the 17 species investigated also showed differential germination along the hydrological gradient. We found a clear linear relation between species hydrological niche as expressed by their Ellenberg F-value and the water level that yielded optimal germination (Fig. 2b; $R^2 = 0.50$, d.f. = 15, $P < 0.001$, $Y = -1.2 + 0.1X$).

LITERATURE DATA

Analysis of literature data on dispersal traits and Ellenberg values of 267 species showed the same patterns as identified above, although greater variation was observed due to the
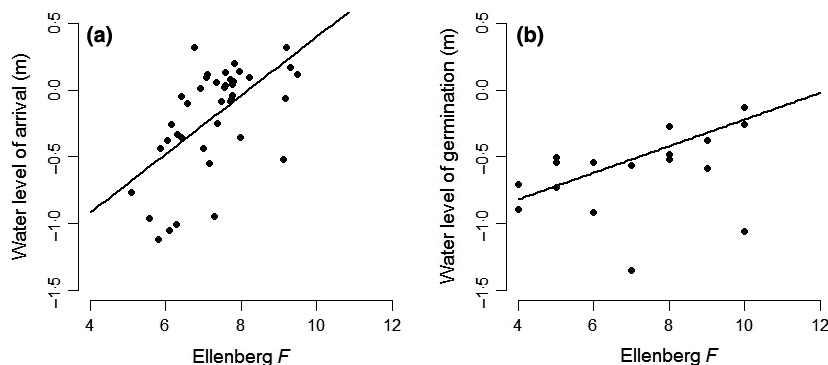
Fig. 2. (a) Seed deposition along the hydrological gradient is related to the hydrological niche of species along the gradient, as approximated by species' Ellenberg F-values. Data points represent community-weighted Ellenberg F-values for all seeds per seed trap. (b) Seed germination along the hydrological gradient is related to the hydrological niche of species along the gradient. Data points represent germination optima for each of the 17 riparian species used in the field germination study.

wide range of wetland communities (and hence, species) included (Fig. 3a,b). The vast majority of species of inundated, submerged niches (Ellenberg F range 12-11) have seeds that immediately sink and can only be dispersed as bed load. Very high dispersal abilities by water (peak buoyancies) occur dominantly in wetland species characteristic of water–land transitions, which include all shorelines (Ellenberg F 10-8). For more terrestrial wetlands (Ellenberg F 7), buoyancies are intermediate (Table S4, quadratic relation $R^2 = 0.35$, d.f. = 145, $P < 0.001$, $Y = -310.8 + 92.4X - 5.5X^2$). Dispersal capacity by wind showed a less clear pattern, with increasing wind dispersal abilities for increasingly drier niches across the range Ellenberg F 12-8, but a levelling-off of this relation at the driest niches (Ellenberg F 7-6) (Table S4, linear or quadratic relation N.S.).

MODEL SIMULATIONS

After 500 generations, a stable pattern evolved in which selection for water dispersal ability resulted in a unimodal relation between niche and buoyancy (Fig. 4a; Table S4, $R^2 = 0.13$, d.f. = 21001, $P = < 0.001$, $Y = 31.5 - 86.7X - 65.1X^2$). Plants characterized by fully inundated hydrological niches very rapidly evolved seeds that sink immediately, because any individuals with floating seeds 'lost' seeds that were deposited on the bank along the fluctuating waterline. The evolved buoyancy increased along with the hydrological niche towards peak buoyancies for plants growing at the waterline, ensuring final deposition of their seeds at or near the waterline. The long floating times resulted in widely scattered seed deposition patterns per individual

along the waterline, increasing the probability of finding suitable sites and reducing the risk of sibling competition for these plants occupying a narrow (spatially scarce) niche. Plants of more terrestrial niches showed random buoyancies with large variation, reflecting a lack of selection for water dispersal ability and limiting the predictive value of the function (R^2).

Independent of water dispersal abilities, wind dispersal abilities resulting after 500 generations were also strongly related to water level (Fig. 4b; Table S4, quadratic relation but monotonously declining, $R^2 = 0.79$, d.f. = 21001, $P = < 0.001$, $Y = 1.8 - 2.5X - 0.8X^2$). Wind-dispersed plants above the waterline increased the probability of finding suitable sites and reduced sibling competition of their offspring by increasing dispersal distances of seeds through the air. Maximal advantageous dispersal distances were spatially limited by niche breadth, so that plants with increasingly terrestrial niches (which were set to be wider further from the stream, to simulate a gradually levelling v-shaped stream valley) had increasing wind dispersal abilities.

Simulation results were robust to changes in model settings, with model fits (R^2) increasing substantially when more generations were simulated (Appendix S7), except for the setting of including a natural, gradually levelling, v-shaped stream valley, which was a critical factor driving long-distance dispersal strategies (Appendix S7).

Discussion

Across the different steps of our tiered approach, we found evidence supporting directed dispersal of water-dispersed
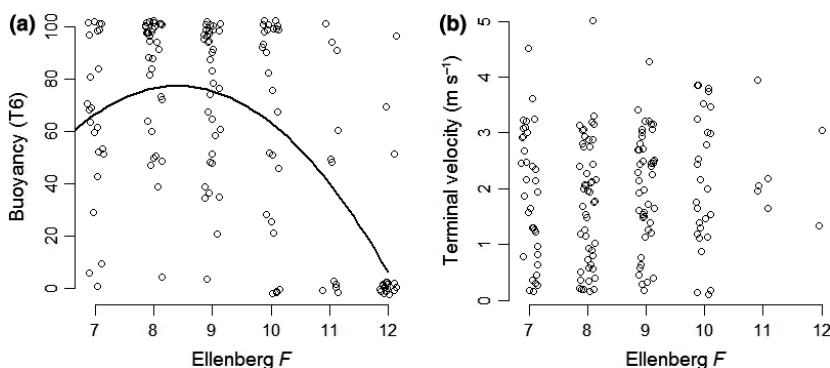

Fig. 3. Ability for dispersal by water and wind varies with hydrological niche across plant species from 21 wetland communities. (a) Ability for dispersal by water as indicated by seed buoyancy (expressed as percentage of seeds remaining afloat after 1 week in water). (b) Ability for dispersal by wind as indicated by seed terminal velocity. Data from literature (data bases PLANTATT and LEDA, see text). Data points are jittered along the x-axis.

Fig. 4. Model simulations show that natural selection for seed buoyancy (a) and terminal velocity (b) is likely to occur for species growing under inundated conditions (selection for low buoyancy), at shorelines (selection for very high buoyancy) and at more terrestrial sites (selection for low terminal velocity). Data points represent trait combinations standardized hydrological niche × seed buoyancy and standardized hydrological niche × wind dispersal distance for the individuals in the 500th generation.
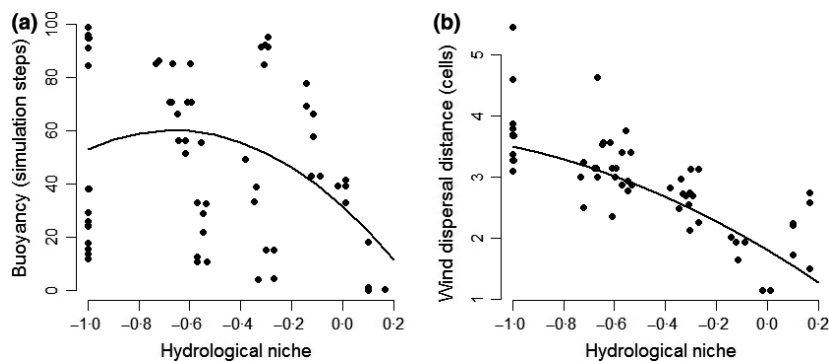

seeds to sites along the hydrological gradient where they have a predictably higher probability of germination and establishment. In summary (Fig. 5), our results indicate that aquatic plant species growing under inundated conditions produce seeds that sink immediately after release into the water, facilitating transport as bed load towards inundated sites. In contrast, shoreline plant species produce seeds with adaptations to float on the water for very long periods of time, which allows them to remain on the water column until they are eventually entrapped by shoreline vegetation or deposited on the bank. Field data confirm that seed deposition of these species occurs predominantly along the waterline. More terrestrial species produce seeds with very low terminal velocities that allow them to disperse well via wind. These species have widely variable buoyancies, indicating a lack of selective pressure to promote dispersal by water. These patterns are reflected in our literature data analysis and in simulations using our individual-based model.

Until now, the possibility of directed dispersal by water had been postulated, based upon observations, by Fraaije *et al.* (2015b) and it had been suggested to occur in riparian willow species (Seiwa *et al.* 2008). In an experimental setting, the transport of long-floating *Betula* seeds towards the waterline had already been demonstrated (Merritt & Wohl 2002), as well as the relevance of high buoyancy for deposition at the waterline (Van Leeuwen *et al.* 2014). Our combined evidence on the seed traits of 1840 seeds, germination of 5520 seeds of 23 species in the greenhouse and 6120 seeds of 17 species in the field, as well as field trapping data on 18 842 seeds of 110 species and literature data on 267 species, now provides evidence for directed dispersal by water for a wide range of species actually happening in the field. Simulations with our individual-based model provide the theoretical basis for selective pressure on seed traits promoting directed dispersal.

The morphological adaptations underlying the differential abilities for dispersal by water involve more than just specific seed density. While ability to disperse by water is correlated with seed density in most species, for example through possession of air sacs or very light tissues (e.g. Hroudova, Moravcova & Zakravsky 1997), the correlation is poor. Many seeds have other adaptations to promote buoyancy, such as strongly hydrophobic seed coatings (as

Fig. 5. Across wetlands bordering open water, such as stream riparian zones, river floodplains, lake shores and floating fens, directed dispersal by water may be common. Plant species growing under inundated conditions produce rapidly sinking seeds that may be dispersed by water as bed load towards inundated sites. Plant species growing at shorelines produce seeds with extremely high buoyancies that may be dispersed by water on the surface for long periods of time until they become trapped in the shoreline or deposited in the driftline. Plant species growing at increasingly terrestrial conditions increasingly depend on wind for dispersal to similar sites.
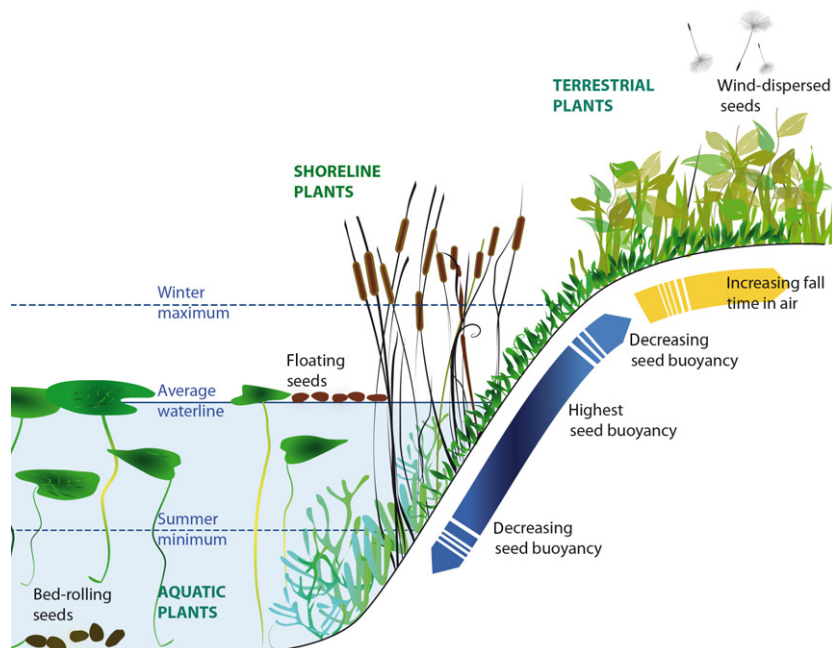
in our species *Lycopus europaeus* and *Lysimachia vulgaris*, Bouman & Meeuse 1992; F. Bouman, pers. comm.) or a water-repellent seed surface microrelief (Bouman & Meeuse 1992), which allow for high floating abilities despite seed densities slightly above the density of water.

Interestingly, seeds with slow falling velocity in water have been demonstrated to be deposited in river flood-plains along with sediments of similar falling velocity (Nakayama *et al.* 2007). This suggests that in high-energy systems (such as rivers), seed deposition patterns are likely to follow sediment deposition patterns and that falling velocity in water may be an additional seed trait determining dispersal by water and deposition patterns. Furthermore, we suggest that the plant traits governing dispersal by water are likely to be adapted to the average or most frequent hydrological conditions and dynamics of a system. For example, during extreme flood events, as witnessed during 1 year at one of our sites (Fig. S6), the high energy of the water may deposit even the largest and most rapidly sinking seeds along the flooded banks.

With respect to directed dispersal by wind, the situation is more complex. Clearly, ability to disperse by wind has evolved predominantly in the most terrestrial of the riparian zone species, for which water dispersal would be ineffective. Indeed, dispersal by wind becomes increasingly common across a range of wetlands from open water to terrestrial banks and uplands (Soons 2006). Wind is the ideal vector for dispersal of seeds over land and across water barriers to reach other more terrestrial areas and is the main mechanism available to traverse between more terrestrial sites in a patchy habitat interspersed with water. However, seed dispersal by wind is not directed dispersal in the strictest sense, as the seeds will reach a range of different habitats. Seed dispersal by wind may be more strictly 'directed' in forests, where model simulations suggest that wind flow deposits aerodynamically adapted seeds of light-demanding species disproportionally in gaps (Nathan *et al.* 2005). Also, wind has been shown to disperse specialized seeds of coastal species predominantly inland, due to non-random abscission (Greene, Quesada & Calogeropoulos 2008), a mechanism that also greatly affects dispersal patterns (Soons & Bullock 2008; Pazos *et al.* 2013). In the investigated wetland situation, wind simply appears to be the best available dispersal vector to reach drier areas in a wetland environment. Clearly, the more terrestrial wetland species included in our study have adapted to wind dispersal. Their seeds possess morphological adaptations to promote dispersal by wind: seeds with such low mass and large diameter have low falling velocities and are dispersed over long distances by wind (Nathan *et al.* 2002; Soons *et al.* 2004).

Interestingly, our model simulations showed that the patterns we find in seed buoyancy and terminal velocity may develop entirely independent of each other – there is no morphological or physiological trade-off required. The relation between seed buoyancy and plant hydrological niche is driven by the combination of benefits of arrival at suitable sites (by directed dispersal) and reduction of sibling competition in spatially narrow niches (long-distance dispersal as bed load or on the water surface). The relation between seed terminal velocity and plant hydrological niche develops independently for terrestrial plant species above the water line, driven by the increasing spatial extent of suitable sites at increasing elevation.

Based on our results, we conclude that the dispersal of many aquatic and shoreline wetland plants by water is a mechanism of directed dispersal *sensu* Howe & Smallwood (1982). We thus demonstrate that directed dispersal of seeds by abiotic vectors is a realistic possibility and we propose that this is likely to be a far more common phenomenon than previously thought. In our study, we focused on wetland types adjacent to open water, where strong hydrological gradients across short spatial scales result in hydrological niche segregation (Silvertown *et al.* 1999) and directed dispersal may be particularly important – perhaps even facilitating niche segregation. Yet, hydrological niche segregation also exists in more terrestrial systems (Silvertown, Araya & Gowing 2015) and at least one study already demonstrated directed dispersal to nearby safe sites by rainwater in a terrestrial *Veronica* species (Pufal & Garnock-Jones 2010).

As water and wind are very common dispersal vectors throughout the plant kingdom (Van der Pijl 1982), directed dispersal, and not just dispersal distance, seems to be of general importance for the ecology of plants and may be a dominating selective force in seed dispersal. Research on seed dispersal should therefore not focus predominantly on understanding dispersal distance distributions, but should include the potential for increased growth and establishment of new individuals achieved by targeted seed dispersal to specific sites (e.g. Sarneel *et al.* 2011, 2014; Fraaije *et al.* 2015b). The latter is likely to affect plant species dynamics in many ways – not only by increasing the success of regional species survival, but also by increasing the rates of species' range expansions. Applying the Seed Disperser Effectiveness (SDE) framework (Schupp, Jordano & Gómez 2010) and inclusion of directed dispersal when considering spatial population dynamics or landscape connectivity (Soons *et al.* 2005; Verhoeven *et al.* 2008) will help to evaluate the consequences of directed dispersal. Dispersal, even by abiotic vectors, is not merely the only way to reach new sites, but also a mechanism to reach the *right* sites.

Authors' contributions

M.B.S. designed the study, analysed data and wrote the manuscript; G.A.dG., M.T.C.R. and R.G.A.F. collected and analysed data; M.dJ. performed modelling work and carried out statistical analyses. All authors contributed to revisions.

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Data accessibility

All experimental data used in this manuscript are present in the manuscript and the Supporting Information.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Species selected for the greenhouse experiments, with data.

Appendix S2. Details on experimental conditions and measurements.

Table S3. Species included in the field germination monitoring.

Table S4. Regression statistics.

Figure S5. Seed buoyancy and terminal velocity explained by seed traits.

Figure S6. Seed deposition of individual species at the restored streams.

Appendix S7. Model sensitivity analysis.

Appendix S8. Worksheet with raw data from the greenhouse experiments.