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1 **Complex interactions between the wind and ballistic seed dispersal in**

2 ***Impatiens glandulifera* (Royle)**

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6 Running headline: *Ballistic dispersal in the wind*

1

2 **Summary**

- 3 1. A mechanistic understanding of seed dispersal is important for understanding and predicting
4 dispersal patterns and spatial population dynamics. We analysed a mechanistic model for the
5 ballistic dispersal of the widespread invasive species *Impatiens glandulifera*. The model
6 deterministically simulates individual seed trajectories, including the interaction between seeds
7 and atmospheric winds. It is fully specified using independently measured plant traits and wind
8 velocities.
- 9 2. To parameterise the model we conducted field surveys and analysed high speed video footage
10 of seed release. We explicitly incorporated intraspecific variation in key biological parameters
11 (seed size and mass, release height, velocity and direction), as well as variation in wind
12 velocities. This parameter variation introduces process-based stochasticity to the deterministic
13 model, allowing the derivation of population-level dispersal kernels.
- 14 3. Analysis of the parameterised model showed complex interactions between plant dispersal
15 parameters and wind conditions. For example, the optimal seed launch angle in still wind is 32°
16 above horizontal, but this rises in stronger tailwinds. In a headwind, it can be optimal to either
17 launch the seed straight upwards or slightly below the horizontal. Headwinds also blow
18 projected seeds back towards the source, initially decreasing but then increasing net dispersal
19 distance, which can reverse the positive effect of seed release height on dispersal distance.
- 20 4. To validate the model we performed a field experiment in which seeds were trapped up to 6 m
21 from potted *I. glandulifera* plants. Seed dispersal was biased in the direction of the prevailing
22 wind, which was only reproduced by simulations of the model that included the wind-
23 modification of ballistic trajectories. The correspondence between the model and the data was
24 good ($R^2 = 0.882$), but improved if seed release was biased to occur in more windy conditions
25 ($R^2 = 0.945$) as might occur through mechanical disturbance to the seed pods.

1 5. **Synthesis:** Our validated model provides a functional understanding of seed dispersal in *I.*
2 *glandulifera*. The model reveals surprisingly complex interactions between the ballistic dispersal
3 mechanism and the wind and shows how population-level dispersal patterns emerge from
4 intraspecific variation in dispersal traits.

5 **Key words:** dispersal, invasion ecology, long-distance seed dispersal, migration, propagule pressure,
6 seed dispersal kernel, wind dispersal.

7

1

2 **Introduction**

3 Seed dispersal is a fundamental process in plant ecology, impacting individual fitness, population
4 dynamics, community structure, gene flow and evolutionary processes (Cousens *et al.*, 2008, Levin *et*
5 *al.*, 2003). As such, it has wide-ranging consequences for invasive species distributions and
6 conservation ecology. Given its significance, much effort has been applied to the study of seed
7 dispersal (Bullock *et al.*, 2006). This includes measurement of seed deposition patterns at varying
8 distance from parent plants in order to provide data on how far seeds are actually dispersed. These
9 data are often then modelled using phenomenological dispersal kernels (e.g. Dalling *et al.*, 2002,
10 Clark *et al.*, 2005) or mechanistic models that incorporate physical factors affecting seed movements
11 and predict dispersal patterns based on measured seed parameters and environmental conditions
12 (Katul *et al.*, 2005, Kuparinen, 2006, NathanSafriel *et al.*, 2001). Mechanistic models are often
13 considered superior to phenomenological approaches since they provide a generalised
14 understanding of the dispersal process in which spatio-temporal variation in dispersal patterns is
15 implicit (Kuparinen, 2006). Although labour-intensive dispersal data are needed to adequately
16 parameterise and validate such models, they can predict dispersal in novel settings more readily
17 than phenomenological models.

18 Ballistic dispersal, where seeds are projected from the parent plant via explosive release
19 mechanisms involves both physical and biological parameters that may be well suited to a
20 mechanistic approach (Beer and Swaine, 1977, Stamp and Lucas, 1983). Using seed dispersal models
21 based on the physical laws of projectile motion, it should in theory be possible to predict dispersal
22 distance and direction from information on the size and shape of the seed, along with its initial
23 projection velocity, angle and height (Beer and Swaine, 1977, Garrison *et al.*, 2000, Hayashi *et al.*,
24 2009, Robinson and Geils, 2006, Vogel, 2005). However, despite the relative tractability of ballistic
25 dispersal we know of only one study that has attempted to validate such models by comparing
26 observed dispersal patterns to those predicted by a ballistic model. Swaine and Beer (1977)

1 recorded the pattern of seed rain around a single *Hura crepitans* L. tree. This exhibited a bimodal
2 pattern with one peak centred roughly at the modal distance predicted by their parameterised
3 model (30 m) and a second peak about the parent tree (interpreted as seeds rebounding from
4 collisions with the tree crown).

5 One complicating factor in ballistic seed dispersal models that has yet to be addressed is that seeds
6 do not disperse through still air conditions but into winds. This has been extensively studied for
7 conventionally wind-dispersed seeds (Horn *et al.*, 2001, Katul *et al.*, 2005, Okubo and Levin, 1989,
8 Schurr *et al.*, 2008, Skarpaas *et al.*, 2006), suggesting that wind conditions can often be more
9 important than plant or propagule characteristics in determining seed dispersal distances.
10 Ballistically dispersed seeds are generally heavier and suffer lower drag than wind-dispersed seeds,
11 but it is still highly likely that the wind will interact with their trajectory during dispersal. Indeed,
12 during windy conditions ballistically-dispersed *Arceuthobium tsugense* (Rosend.) G.N. Jones seeds
13 exhibited an anisotropic dispersal pattern more concentrated towards the prevailing downwind
14 direction than was observed during calm conditions (Smith, 1973).

15 This study considers ballistic dispersal of *Impatiens glandulifera* Royle, which is a widespread and
16 extensive invader of riparian habitats in the UK and much of Europe (Beerling and Perrins, 1993). The
17 *I. glandulifera* seed pod is 1.5–3.5 cm long with five outer valves that rapidly coil upwards during
18 dehiscence, ejecting the seeds. Most seeds land within 3 m of the parent plant, although new
19 seedlings may be found up to 10 m from the nearest potential parent (Beerling and Perrins, 1993).
20 At a national scale, the rapid spread of *I. glandulifera* outstrips the range of ballistic dispersal, and is
21 more likely due to human-aided movement and dispersal within watercourses (Pysek and Prach,
22 1995). However, understanding its primary ballistic dispersal mechanism remains important for
23 predicting local invasion dynamics and is a mechanism by which seeds are deposited into
24 watercourses to become long distance dispersers. It is therefore likely to be an important
25 consideration when devising effective spatially-explicit control measures.

1 Our aim was to analyse the interactions between ballistic dispersal and wind and examine how
2 population-level dispersal patterns may emerge from intraspecific variation in dispersal traits.
3 Specifically, we: (i) adapt ballistic equations for projectile motion to incorporate wind effects; (ii)
4 parameterise the model through quantification of key dispersal traits and wind conditions; (iii)
5 analyse the behaviour of the model to examine interactions between seed traits, the ballistic
6 dispersal mechanism and the wind; and (iv) conduct a seed trapping experiment to validate
7 predictions of the model.

8 **Methods**

9 *Ballistic dispersal model*

10 We simulated seed dispersal by adapting the equations of Hayashi, Feilich & Ellerby (2009)
11 previously used for modelling seed dispersal in *Impatiens capensis* Meerb. In overview, seeds are
12 represented as spheres in 3-dimensional space and are launched from the parent plant at a
13 particular initial velocity, pitch (angle from horizontal), direction (horizontal angle from north) and
14 height. Subsequently, the seed is accelerated by drag and gravity forces (Fig. 1), causing deviation
15 from its initial trajectory that allows us to project its flight through space. We assume that
16 acceleration due to the buoyancy or lift forces are negligible. Once the seed reaches the height of
17 the surrounding vegetation we assume it is intercepted, terminating further movement in the
18 horizontal plane and ending primary dispersal.

19 Consider a spherical seed of mass m (kg) and diameter d (m) travelling through the air with an
20 instantaneous 3-dimensional velocity vector \mathbf{v} (ms^{-1}). At seed height, z (m), the wind has a velocity
21 vector $\mathbf{u}(z)$ (ms^{-1}). The drag force acting on the seed in all three dimensions, f_D (N), is:

$$22 \quad f_D = \frac{C_D \rho A v_R^2}{2}$$

23 where ρ is the air density (set at 1.204 kgm^{-3} , equivalent to $20 \text{ }^\circ\text{C}$ and 100 kPa pressure), A is the
24 seed's frontal area ($\pi d^2/4 \text{ m}^2$) and \mathbf{v}_R is the resultant velocity relative to the wind, $\mathbf{v} - \mathbf{u}(z)$ (ms^{-1})

1 (Vogel, 1988). C_D is the coefficient of drag, which we estimate as a function of the Reynolds number
2 Re as:

$$3 \quad C_D = 0.4 + \frac{24}{Re} + \frac{6}{1 + \sqrt{Re}}$$

$$4 \quad Re = \frac{\rho d}{\mu} \sum \sqrt{V_R^2}$$

5 where μ is the viscosity of the air (set at $1.8 \times 10^{-5} \text{ Nsm}^{-2}$, equivalent to 20 °C) (Vogel, 2005). Varying
6 the air density and viscosity over values for temperatures between 0 and 35 °C causes less than
7 10 cm of total variation in modelled seed dispersal distances, justifying our use of constants for
8 these variables.

9 The gravity force f_G accelerates the seed downwards in the vertical dimension with a force of mg (N)
10 ($g = 9.81 \text{ ms}^{-2}$) and takes a value of 0 in both horizontal dimensions. Thus, the instantaneous change
11 in the seed's velocity is:

$$12 \quad \frac{dv}{dt} = \frac{f_D - f_G}{m}$$

13 The minus sign for f_G signifies its downwards action in the vertical dimension. The trajectory of the
14 seed is simulated from this expression, by numerical integration using Euler's method and a 0.002 s
15 time step. We investigated alternative time steps and found that below 0.002 s there was almost no
16 difference in the resulting dispersal distances, while distances were under-estimated for longer
17 intervals. Integration is terminated when the seed reaches the height of the surrounding vegetation
18 (or bare ground), allowing us to calculate the dispersal distance of the seed in the horizontal plane.

19 Effects of the wind are incorporated via the drag force, since drag accelerates the seed in the
20 opposite direction to its resultant velocity relative to the wind (Fig. 1). For simplicity, we do not
21 include temporal changes in the wind vector during the dispersal of any one seed and assume that
22 wind flow is non-turbulent. We also assume that wind speed increases with height (z) following a
23 logarithmic profile typical of open habitats (Oke, 1987) as:

$$u(z) = \begin{cases} \frac{u^* \ln\left(\frac{z - z_d}{z_0}\right)}{\kappa} & \text{if } z \geq z_d + z_0 \\ 0 & \text{if } z < z_d + z_0 \end{cases}$$

1

2 where z_0 is the roughness length of the vegetation or ground surface (m), scaling the drag exerted by
 3 the surface on the wind. In the model we use an empirical approximation for natural vegetation to
 4 estimate $z_0 = \max(z_{veg}/10, 0.003)$, where z_{veg} is the height of the surrounding vegetation (m) (Oke,
 5 1987). Parameter z_d is the displacement height of the vegetation and represents the height below
 6 which $U = 0 \text{ ms}^{-1}$. The empirical approximation of $z_d = \frac{2}{5}z_{veg}$ is used in the model (Oke, 1987). κ is the
 7 von Kármán constant, which takes a value of 0.41, and u^* is the friction velocity of the air. Friction
 8 velocity characterises the shear stress of the air as it passes over the surface and is calculated by
 9 rearranging the above equation so that u^* is on the left hand side and then entering a value of u at
 10 known z . We had wind speed data for a height of 2.5 m (see below), and so this was used as the
 11 reference height.

12 *Parameterisation*

13 To acquire information on seed mass and shape, 60 balsam plants from a naturalised population on
 14 the River Esk (Musselburgh, Scotland, 3°3'W 55°55'N) were selected in August 2009. These plants
 15 were cut near their base, stood in water and brought back to the laboratory. A ripe seed pod from
 16 each of these was opened and three mature seeds randomly sampled ($n=180$). Seeds were
 17 immediately weighed to the nearest 0.1 mg and the side and top profiles were photographed under
 18 x10 magnification. From this, we estimated the minimum and maximum frontal areas presented by
 19 each seed. In the model, we set spherical seed diameters to the mean of these two frontal areas,
 20 since *I. glandulifera* seeds rotate in the air similarly to *I. capensis* seeds (Hayashi *et al.*, 2009). Seed
 21 release heights were estimated by measuring the height of 2819 dehisced pods to the nearest 5 cm
 22 on a further 60 plants used in a seed trapping experiment (see below).

23 Seed release parameters were obtained by analysing slow motion video footage of the dehiscence of
 24 170 seed pods from different plants to those described above. Digital videos were taken using a

1 Phantom Miro 4 camera (Vision Research, UK) with a frame resolution of 800x600 pixels, frame rate
2 of 1000 Hz and exposure of 40 μ s. The camera was mounted directly above the seed pod and faced
3 downwards in order to view the horizontal plane. One 500 W and two 150 W lamps were used to
4 illuminate the arena and a mirror was mounted at 45° to the horizontal, allowing a simultaneous
5 view of the vertical plane in the camera's field of view. A marked ruler was positioned adjacent to
6 the seed pod as a scale marker.

7 *I. glandulifera* plants were brought into the laboratory from the field site and all leaves and pods
8 except for the ripest pod were removed. Plants were then stood in water for a maximum of 5 hours
9 before use in the experiment, which did not cause any visible wilting. To record pod dehiscence, the
10 plant stem was cut approximately 3 cm below its terminal node and the remaining 3 cm of stem was
11 mounted vertically in a retort stand at bench level under the camera. In this way the pod's typical
12 attitude relative to the stem was maintained and the natural recoil ability of the peduncle (flower
13 stalk) was also retained. A pair of fine forceps was used to apply light pressure to a single pod outer
14 valve at its proximal end (i.e. near the peduncle) to trigger dehiscence. Any pods not dehiscing under
15 the light pressure were rejected, ensuring that only fully ripe pods were included in the study. The
16 proximal end of the pod was manipulated as *I. glandulifera*'s dispersal mechanism is for the turgid
17 outer pod valves to coil upwards and eject the seeds (Hayashi *et al.*, 2009 describe a similar
18 mechanism). In preliminary trials we found that manipulating the distal end of the pod interfered
19 with this coiling mechanism and slowed the seed release. Video frames were imported into ImageJ
20 v.1.42q (Rasband, 1997-2011) and a single seed was randomly selected from each pod, excluding
21 any that collided with the forceps. The change in position of the seed over the first two frames in
22 which it was clearly separated from the pod was used to estimate its launch velocity and pitch. The
23 pod length and orientation prior to dehiscence was also estimated from the footage.

24 To characterise intraspecific variation in these parameters we fitted flexible statistical distributions
25 to the data, by a maximum-likelihood simplex algorithm (Nelder and Mead, 1965). Seed masses,
26 release heights and launch velocities were characterised with Gamma distributions since they

1 cannot take negative values. Seed pitches were characterised with a Cauchy distribution, truncated
2 between -90° and 90° from the horizontal. This distribution was used as it is flexible enough to
3 represent a range of unimodal distributions constrained over a fixed range (Nadarajah and Kotz,
4 2007). Seed diameters were found to exhibit a strong correlation with mass, and so a nonlinear
5 power relationship was fitted by least squares and the residuals modelled as a Gaussian distribution.

6 *Model validation*

7 A seed trapping experiment was conducted to validate model predictions. In April 2010 seedlings
8 were collected from the River Esk site and transplanted into 12 pots (26 cm diameter) filled with
9 sand and compost (1:1 by volume) at an evenly spaced density of 5 seedlings per pot. These plants
10 were grown in an unheated glass house with ad hoc but equitable watering and fertilisation. On 15th
11 August 2010, when plants were beginning to produce mature seed pods, the pots were moved to a
12 mown grass field (Midlothian, Scotland, $3^\circ 12' 13'' \text{W}$ $55^\circ 51' 43'' \text{N}$). The 12 pots were dug into the
13 ground at 50 cm intervals in a line perpendicular to the direction of the prevailing wind (blowing
14 from 210° over the previous 10 years, see below). To prevent the *I. glandulifera* stems breaking
15 under high wind conditions, a bamboo cane was planted in each pot and the plants were loosely
16 bound with string.

17 The seed traps were rectangular plastic trays (30 x 40 x 10 cm) filled with water to a depth of at least
18 5 cm throughout the experiment. Thirty traps were arranged in a line running perpendicular to the
19 row of balsam pots (i.e. aligned with the prevailing wind) and through their centre. There were 15
20 traps on each side of the pots evenly spaced at 40 cm intervals so that trap centres were between
21 0.25 and 5.95 m from the line of pots. Preliminary simulations of the dispersal model, performed
22 prior to the experiment as recommended by Skarpaas *et al.* (2005), suggested that very few seeds
23 would be trapped at greater distances than this. Between 16th August and 28th September 2010 the
24 traps were checked daily (excluding weekends) and all seeds were collected. By the end of the
25 experiment there were very few intact seed pods remaining. The number and heights of all dehiscid

1 seed pods were determined from the stalks remaining after dehiscence (see above). These were
2 recorded to replicate the starting positions of seeds in the experiment during model simulations.

3 Raw data from seed trapping experiments do not give dispersal kernels (i.e. frequency or probability
4 distributions of dispersal distances) because of the observational bias introduced by the trapping
5 design (see Chapter 5 in Cousens *et al.*, 2008). To correct this bias and validate the model
6 predictions, simulations were designed to mimic the seed trapping experiment. In each simulation
7 run, a seed with random size and mass (drawn from the fitted distributions described above) was
8 assigned to a randomly selected pod dehiscing over the course of the experiment. The pod height
9 was known, but its exact horizontal position was not, and so we set this to a randomly generated
10 coordinate within the relevant pot. The seed was then launched with a randomly drawn velocity,
11 pitch and bearing and a randomly selected wind vector (see below) and if it landed within the area
12 covered by one of the seed traps it was retained. We repeated this until the number of seeds
13 trapped in the simulation equalled the number trapped in the experiment. The whole procedure was
14 repeated 10000 times to obtain 95th percentile ranges for the numbers of seeds collected from each
15 trap. These were then compared with the observed data. Because this process required the
16 modelling of millions of seed dispersal events, we increased the model's computational efficiency by
17 training neural networks to accurately predict the dispersal distance and bearing of seeds from the
18 model parameters (see Appendix S1 of the Supporting Information).

19 Horizontal and vertical wind conditions during the simulations were randomly drawn from observed
20 wind vectors recorded during the experimental period. We randomly sampled wind vectors rather
21 than statistically model them to preserve complex correlation structures between wind velocities
22 and directions that would be difficult to reproduce. Wind vectors were obtained from a Metek
23 USA-1 Sonic anemometer mounted 2.5 m above the ground at a weather station approximately
24 400 m from the experimental set up. Measurements were recorded at 30 minute intervals, but the
25 data contained a gap between 25 August and 16 September when the sensor was non-operational.

1 We therefore assume that wind conditions during the operational period were representative of
2 those in the non-operational one.

3 We also performed a simulation where seeds were dispersed preferentially into strong winds. This
4 was done as *I. glandulifera* seed pod dehiscence may be triggered by physical disturbance during
5 windy conditions. As such, a random sample of the wind vectors may not be representative of those
6 experienced during seed dispersal. In this simulation, wind vectors were sampled with an arbitrarily
7 chosen weighting proportional to their absolute magnitude, i.e. the probability of selecting a
8 particular vector was its magnitude divided by the sum of all wind vector magnitudes.

9 **Results**

10 *Model parameterisation*

11 Summaries of measured seed masses, diameters and release heights are given in Table 1. There was
12 a strong correlation between mass and diameter ($r = 0.972$, $P < 0.001$), with the relationship well
13 captured by the fitted power function ($R^2 = 0.959$, see Table 1). Seeds were released with a median
14 velocity of 6.2 ms^{-1} and a median pitch of 48° above horizontal (Table 1). The maximum observed
15 velocity was 12.4 ms^{-1} and there was a tendency for greater launch speeds from longer seed pods
16 ($r = 0.454$, $P < 0.001$). Seed launch pitches were also strongly correlated to the pitch of the pod prior
17 to dehiscence ($r = 0.736$, $P < 0.001$) and we observed a weak negative correlation between launch
18 pitch and velocity ($r = -0.159$, $P < 0.039$). Intraspecific variation in these parameters was well
19 captured by the fitted distribution functions (Table 1), as evidenced by non-significant Kolmogorov-
20 Smirnov tests against the theoretical distributions (all with $P > 0.393$). The one exception to this was
21 for seed release heights ($P < 0.001$) for which the quantiles were highly correlated (every 0.01 from
22 0.01 to 0.99, $r = 0.984$) but there was a very large sample size ($n = 2819$).

23 *Analysis of the parameterised model*

24 In still air, dispersal distances calculated by the model increased with seed mass, launch height and
25 launch velocity (Fig. 2a–c), while the optimal launch angle was around 35° above horizontal (Fig. 2c).

1 The dispersal of light seeds was more strongly influenced by the wind than that of heavy seeds (Fig.
2 2a and e) and a tailwind reversed the relationship between release height and dispersal distance
3 from positive to negative (Fig. 2b). Dispersal distance in the model increased with increasing
4 horizontal tailwind speed (direction = 0° in Fig. 2d). However, with a horizontal headwind
5 (direction = -180° or 180° in Fig. 2d) dispersal distances were curtailed up until a point where the
6 wind blew the seed in the opposite direction in which it was launched. Higher vertical wind speed
7 increased dispersal distance in a tailwind, especially for light seeds, but had little effect in a
8 headwind other than for the lightest seeds (Fig. 2e). These relationships illustrate the complex
9 interactions between ballistic seed release and the wind that are likely to determine patterns of *I.*
10 *glandulifera* dispersal (Fig. 4).

11 *Model validation*

12 During the seed trapping experiment (when the anemometer was operational), the median
13 horizontal wind velocity was 2.92 ms⁻¹ (95th percentile range 0.34-6.17 ms⁻¹) and the median vertical
14 wind velocity was -0.037 ms⁻¹ (95th percentile range -0.107-0.107 ms⁻¹). The circular mean wind
15 direction was 245° (circular variance = 32.0°), although the distribution of wind directions was
16 actually bimodal with a major peak around 210° and a minor peak at approximately 25°. Thus as
17 expected, seed traps were aligned with the prevailing wind.

18 Over the experimental period 507 seeds were collected, mainly in traps close to source plants (Fig.
19 5). Significantly more seeds were found in traps downwind of the prevailing wind than those upwind
20 of it (369 vs. 138, $\chi^2_1 = 105$, $P < 0.001$). Simulations of the model that did not include any interaction
21 between the wind and seed trajectories did not reproduce this asymmetric pattern and gave a poor
22 fit to the observed data (Fig. 4). By contrast, simulations of the dispersal model that included the
23 wind effect gave a much better fit, with 24 of the 30 observed seed trap counts lying within the 95th
24 percentile range of model predictions (Fig. 5b). However, there appeared to be a slight tendency for
25 greater downwind dispersal in the data than was produced by the model. It is possible that this is

1 caused by a higher likelihood of pod dehiscence with increased physical disturbance during windy
2 conditions. Indeed, biasing seed release to occur more frequently during high winds improved model
3 fit (Fig. 5c). In this case 28 of the 30 trap counts were within the 95th percentile range of the
4 simulated data.

5 **Discussion**

6 Our model for the primary dispersal of *I. glandulifera* seeds through ballistic release, and
7 experimental results, suggest that *I. glandulifera* seeds are rarely dispersed further than 6 m. This
8 supports the prevailing view that ballistic dispersal is an efficient but relatively short-distance
9 dispersal mechanism (Cousens *et al.*, 2008, Stamp and Lucas, 1983). However, unlike other similar
10 models (Garrison *et al.*, 2000, Hayashi *et al.*, 2009) we explicitly incorporated the effects of wind
11 flow on modelled seed trajectories. Our results suggest that failing to include this seed-atmosphere
12 interaction means that models will be unable to reproduce the clear dispersal bias in the direction of
13 the prevailing wind (see seed trapping experimental results). By contrast, simulated seed trapping
14 patterns produced with wind vectors recorded at the experimental site closely matched the
15 observed pattern, demonstrating the important role of wind in the primary dispersal of *I.*
16 *glandulifera*.

17 Analysis of the dispersal model revealed a surprising array of complex interactions between plant
18 dispersal traits and the wind (see Figs 2–3). In the main, modelled relationships between traits and
19 dispersal distances produced in still air were qualitatively similar to those produced with tailwinds,
20 but with increased dispersal distance. For example, heavier seeds were dispersed further in both
21 situations because of lower relative drag compared to light seeds. This relationship could only be
22 reversed by strong updrafts, in which the higher drag of light seeds retarded their rate of descent
23 under gravity allowing further dispersal. However, the most complex behaviour of the model was
24 observed when the orientation of the wind was varied from the direction of the seed. Tailwinds blew
25 seeds back towards the point they had been launched from. Ignoring any interception by the parent

1 plant, this caused a non-linear effect of tailwind velocity on net dispersal distance, characterised by
2 an initial decrease and then increase with progressively stronger winds. Tailwind was also able to
3 reverse the otherwise positive effect of seed release height on dispersal distance. The reason for this
4 is that the increase in wind velocity with height above the ground (NathanHorn *et al.*, 2001, Oke,
5 1987) meant that taller plants launched their seeds into stronger tailwinds. This resulted in a slightly
6 lower dispersal distance for a typical seed, although it may be that very light seeds could be carried
7 further in the downwind direction when released at height.

8 Another consequence of the height-variation in wind velocity was to alter the 'optimal' seed launch
9 pitch, i.e. the initial launch angle resulting in the greatest dispersal distance. In still air the optimal
10 pitch was $\sim 35^\circ$ above the horizontal, which is similar to values estimated for other ballistically
11 dispersing seeds (Garrison *et al.*, 2000, Hayashi *et al.*, 2009, Vogel, 2005) but shallower than the
12 median pitch of 48° observed in the seed release high speed videos. However, our model shows how
13 such estimates of optimal pitches are overly simplistic, since the optimal pitch varies dramatically
14 with the strength and orientation of the wind (see Fig. 3). As headwinds increase there is an
15 advantage in exposing the seed to the greater wind velocities that occur higher above ground.
16 Therefore the optimal pitch steepens. Under a pure tailwind the opposite is true so that optimal
17 pitch decreases with velocity, eventually falling below the horizontal. When there is a strong
18 crosswind it becomes optimal to launch the seed vertically, maximising its exposure to the wind but
19 imparting no horizontal movement. In this case all horizontal dispersal achieved by the seed will
20 result from it being carried on the wind. Launch pitch may be a readily adaptable trait because of the
21 strong correlation we found between pitch and seed pod orientation, which may be under heritable
22 genetic control. Therefore, we suggest that *I. glandulifera* has evolved a steeper pitch than is optimal
23 under still air conditions in order to increase the chance that seeds achieve high trajectories and can
24 increase their dispersal distance if encountering favourable winds.

25 Although our model simulates the trajectory of individual seeds deterministically, we incorporated
26 process-based stochasticity via intraspecific variation in seed dispersal traits and by randomly

1 sampling wind velocity vectors. This meant that dispersal kernels could be derived by simulating
2 large numbers of dispersal events (see Fig. 4). We have produced population-level kernels but
3 individual-level kernels could also be derived (Thiede and Augspurger, 1996). These kernels vary with
4 local meteorological conditions and the distribution of dispersal traits among the focal population or
5 individual. For example, the observed unimodal distribution of *I. glandulifera* launch pitches (angles
6 relative to horizontal) generated unimodal dispersal kernels, rather than the bimodal kernels
7 imparted by uniform pitch distributions (Beer and Swaine, 1977, Neubert and Parker, 2004, Rezvani
8 *et al.*, 2010). Spatio-temporal variation in meteorological conditions and plant traits, either through
9 phenotypic plasticity or local adaptation, will therefore cause dispersal kernels to vary greatly in
10 space and time (Bullock *et al.*, 2003, NathanHorn *et al.*, 2001). For example, *I. glandulifera* adapts to
11 northerly latitudes by growing to a shorter height (Kollmann and Bañuelos, 2004) and produces
12 heavier seeds in cooler temperatures (Willis and Hulme, 2004). We have also observed that shaded
13 plants grow to be taller but produce shorter seed pods (D. Chapman unpublished data), which will
14 impart lower launch velocity. This intraspecific variability in response to environmental gradients
15 highlights the importance of the mechanistic approach to seed dispersal modelling (Katul *et al.*,
16 2005, Kuparinen, 2006). In principle, our model provides a functional understanding of dispersal
17 which can accommodate between-individual and between-population variation in dispersal kernels
18 caused by both trait variation and abiotic gradients. However, a limitation of our study is that we did
19 not model the hierarchical or nested structure of variation in seed traits (within-pod) or pod traits
20 (within-plant, within-population), other than for the distribution of seed release heights (where it is
21 implicit that there is no within-pod variability). This was because heights were measured for every
22 exploded seed pod on all our experimental plants, whereas the other traits were measured with
23 sampling designs that did not permit such a representation (Table 1).

24 Despite this simplicity, the model gave a good prediction of observed seed trapping patterns.
25 Importantly, the field validation of the dispersal model was totally independent of the theoretical
26 model formulation or its parameterisation. As such the adequate reproduction of observed dispersal

1 distributions suggests that the model captured salient features of the dispersal process. However,
2 we also found that if the model was adjusted so that seed dispersal preferentially occurred during
3 high winds then its fit was improved. Although we have no data to support it, there is good reason to
4 suspect that windy conditions promote pod dehiscence through increased mechanical disturbance
5 that breaks the joints between pod outer valves (Beerling and Perrins, 1993, Hayashi *et al.*, 2009).
6 There may also be a link between dehiscence probability and rainfall or humidity not considered in
7 our modelling. This is because pod valve turgor maintained by plant hydration promotes dehiscence
8 (Hayashi *et al.*, 2009). In *Pinus halepensis*, seeds are disproportionately released when upwards wind
9 movement is highest, which promotes long distance dispersal (Nathan *et al.*, 1999). However, we
10 would not expect a similar pattern in *I. glandulifera* since our model suggests that vertical wind has
11 only a moderate effect on dispersal distance compared to horizontal wind (Fig. 2). Nevertheless, our
12 results add to existing evidence that non-random seed release, with respect to meteorological
13 parameters, is an important but under-studied aspect of seed dispersal (Narbona *et al.*, 2005, Soons
14 and Bullock, 2008, Nathan *et al.*, 1999).

15 At the field site where plants used to parameterise the model were collected, pods contain a mean
16 of 6.8 seeds ($n = 301$, standard deviation = 3.0; D. Chapman unpublished data). This suggests that
17 given the number of dehisced pods counted on our experimental source plants, around 19300 seeds
18 would have been produced. If this number of seeds were dispersed according to our model then we
19 would have expected 1.8–2.1 times as many seeds to have been trapped as were recovered (with
20 the least difference for the wind-weighted model). There are probably two explanations for this.
21 First, seeds in the traps may have been subject to predation, e.g. by birds. Second, some seeds may
22 have collided with the adult balsam plants, fallen to the ground and thus not reached the traps. The
23 experimental set up consisted of a row of 12 pots, each with five *I. glandulifera* plants arranged like
24 the dots on the 5-face of a dice. This formed a more-or-less continuous ‘hedge’ of source plants in
25 which many seeds would have been launched directly towards the parent or another plant. The
26 central plants in each pot were surrounded by neighbours on all sides, while most outer plants had

1 close neighbours on half of their perimeter. Collisions with the parent have also been suggested as
2 important determinants of ballistic dispersal patterns in *Hura crepitans* (Swaine and Beer, 1977),
3 *Oxalis corniculata* L. (Rezvani *et al.*, 2010) and *Cytisus scoparius* L. (Malo, 2004) suggesting that such
4 effects require consideration before mechanistic models are used to predict population dynamics or
5 spread.

6 In conclusion, our validated model provides a functional understanding of primary seed dispersal in
7 *I. glandulifera* that should also apply to other ballistically-dispersed species and reveals a complex
8 array of previously unexplored interactions between ballistic dispersal and the wind. Our results also
9 have a wider relevance for invasive species ecology. For *I. glandulifera*, which is an annual with a
10 transient seed bank and strong local density-dependence (Beerling and Perrins, 1993), local
11 population and invasion dynamics must depend critically on dispersal. As such, our results on
12 primary seed dispersal should be informative for planning management strategies at a local scale,
13 with the strong caveat that secondary dispersal mechanisms including water transport also require
14 consideration (Wadsworth *et al.*, 2000). For example, we predict that within-site invasion speeds
15 should be greatest in the downwind direction relative to the prevailing wind, where the river is
16 aligned to the prevailing wind direction. Under this scenario, the individuals furthest downwind will
17 have the greatest contribution to population growth and so control should target these. Likewise,
18 our modelling shows that plants further than 6 m from the river will deposit very few seeds into the
19 river directly. Thus they may be relatively unimportant for catchment-scale spread, depending on
20 the extent of secondary dispersal due to flooding, animals or surface winds. This illustrates the
21 potential for validated mechanistic dispersal models to be used in planning control strategies for
22 problem invasive species and emphasises that considering interactions between dispersal traits and
23 the wind will be a necessary step towards this goal.

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16

17 **Supplementary material**

18 The following supplementary material is available for this article:

19 **Appendix S1** Neural network approximation to the seed dispersal model

20

1

2 **Tables**

3 **Table 1.** Intraspecific variation in biological parameters of the model, including their median values,
4 variances and statistical distributions used in model simulations. In the case of seed mass, release
5 height, velocity and pitch parameter distributions were fitted to the data by the simplex maximum
6 likelihood algorithm (Nelder and Mead, 1965). The relationship between seed diameter and mass
7 was fitted by nonlinear least squares ($R^2 = 0.959$) and the standard deviation of the residuals used to
8 add stochasticity to the output. Release angles in the horizontal plane were assumed to be uniformly
9 distributed and the vegetation height was set to that during the seed trapping experiment

Parameter	Data source	Median (95 th percentile range)	Total variance	Mean within-sample unit variance	Distribution
Seed mass (mg)	3 seeds from each of 60 pods on different plants (n=180)	20.7 (8.8–38.3)	50.46	20.12	Gamma (shape=8.442, rate=0.396)
Seed diameter (mm)	As above	3.36 (2.53–4.12)	0.162	0.079	Gaussian (mean=1.194×Mass ^{0.342} , sd=6.02×10 ⁻²)
Seed release height (m)	All 2819 pods from 12 plants	1.40 (1.15–1.90)	0.087	0.020	Gamma (shape=19.04, rate=14.16)
Seed release velocity (ms ⁻¹)	1 seed from each of 170 plants (n=170)	6.19 (2.57–10.17)	3.705	Na	Gamma (shape=9.663, rate=1.538)
Seed release pitch (° from horizontal)	As above	47.8 (-37.1–79.7)	639.3	Na	Truncated Cauchy (location=48.47, scale=11.85, min=-90, max=90)
Seed release direction in horizontal plane (° from north)	None (assumed uniform)				Uniform (min=0, max=360)

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2 **Table 2.** Approximate model fit statistics derived by comparing the observed number of seeds per
3 trap to the mean number predicted over 10000 model simulations. R^2 is the squared correlation
4 between observed and expected. An approximate log-likelihood was calculated assuming the
5 observed data are drawn from Poisson distributions with means per trap equal to those simulated.
6 Log-likelihoods were used to estimate the ΔAIC statistic to compare the models ($\Delta AIC = 0$ indicates
7 the most parsimonious model). Finally the χ^2 goodness of fit statistic was calculated, with P values
8 estimated through a Monte Carlo test with 10000 replicates

Model	R^2	Log-likelihood	ΔAIC	χ^2 G.O.F. (P)
No wind effect	0.695	-145.0	116.8	173.7 ($< 10^{-4}$)
Random wind effect	0.850	-99.3	25.4	81.6 ($< 10^{-4}$)
Weighted wind effect	0.903	-87.1	0	54.7 (0.007)

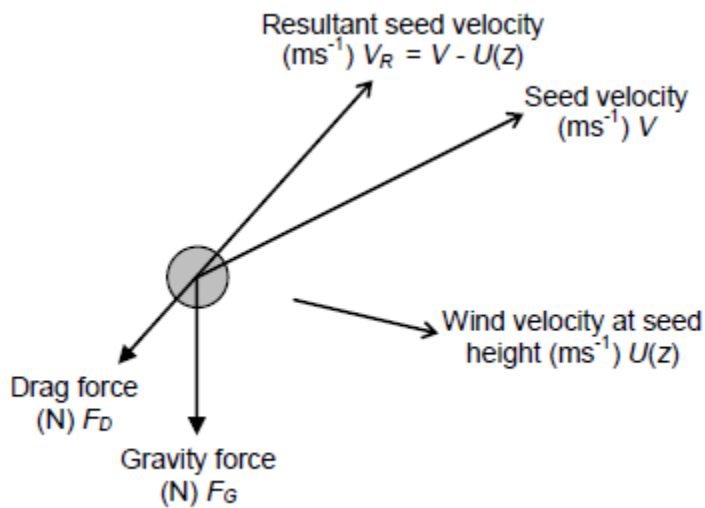
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2 **Figures**

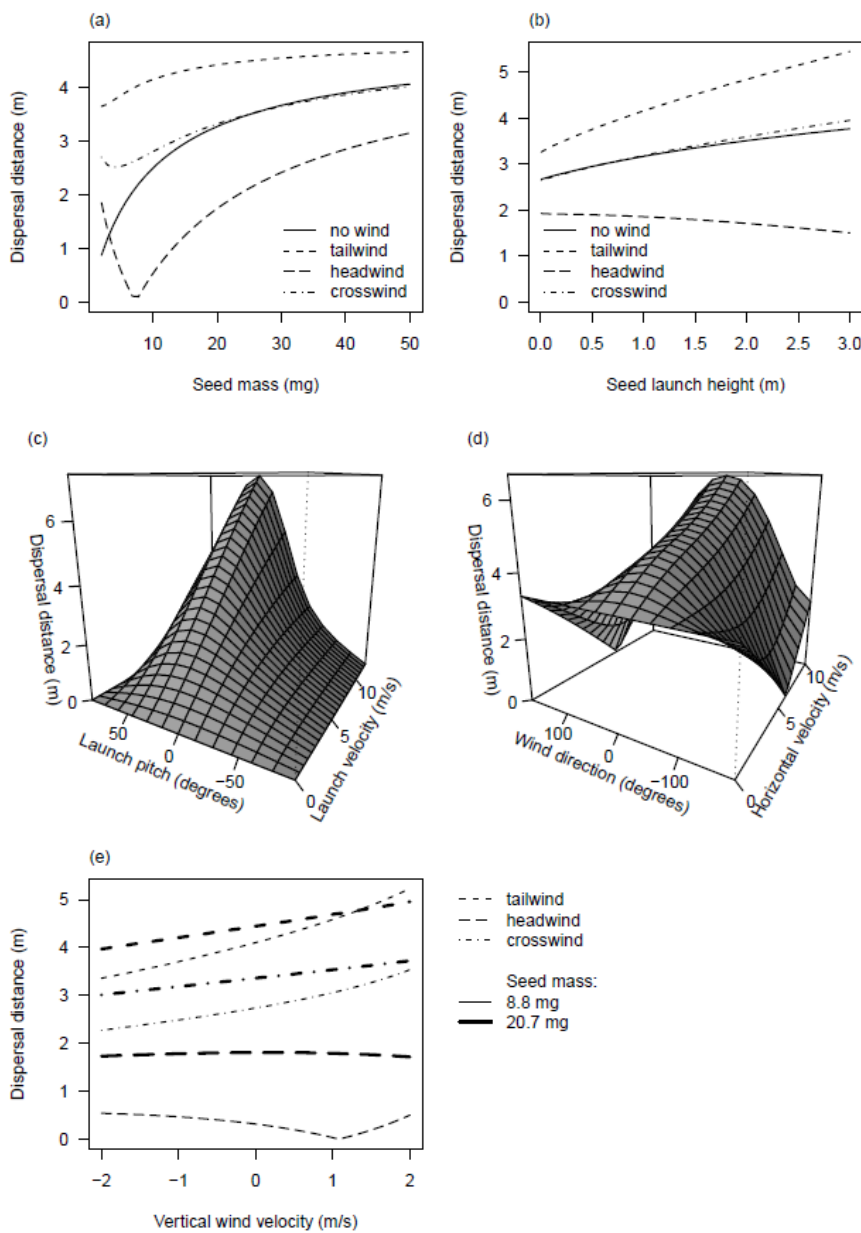
3 **Figure 1.** Schematic of the forces (solid arrow heads, not to scale) and velocities (open arrow heads,
4 to scale) acting on a seed (grey circle) during dispersal in the model (Cousens *et al.*, 2008). All
5 velocities and forces are 3-dimensional vectors. Gravity always accelerates the seed downwards,
6 while drag acts in the opposite direction to the resultant seed velocity, relative to the wind. Wind
7 speed varies as a function of height (z).



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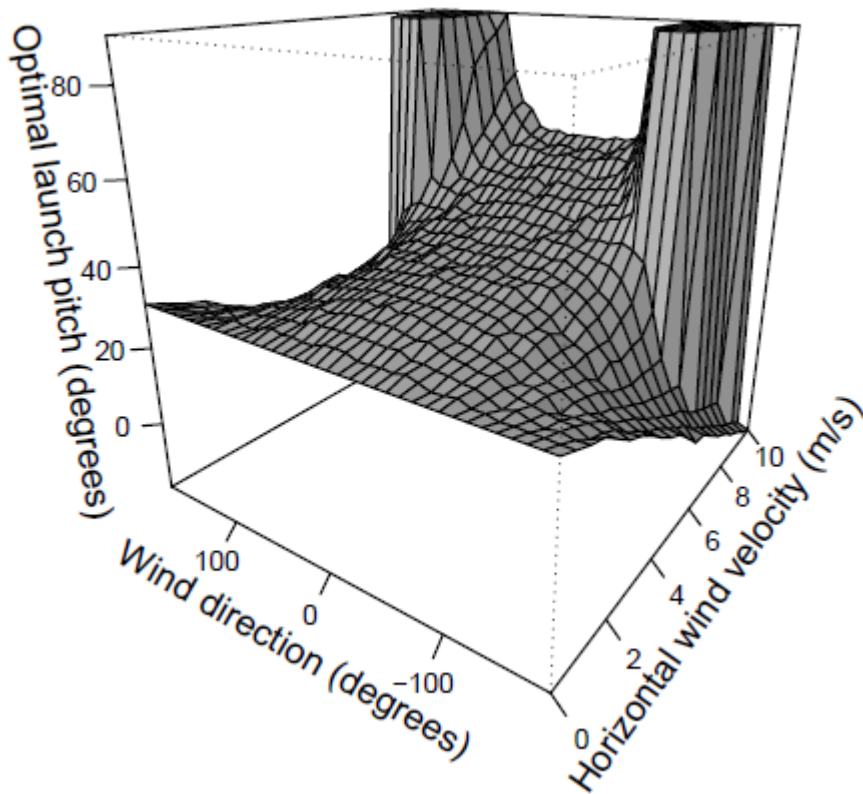
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 2 **Figure 2.** Effects of (a) seed mass, (b) release height, (c) release velocity and pitch, (d) horizontal
 3 wind velocity and direction (relative to the seed's release direction) and (e) vertical wind velocity on
 4 dispersal distances calculated by the model. Plots (a) and (b) display dispersal into still air and 3 ms^{-1}
 5 (at 5 m height) horizontal head, tail and cross winds (i.e. winds oriented at 0, 180 and 90° to the
 6 direction of the seeds' initial projection, respectively). In (e) interactions between seed mass and the
 7 wind are illustrated. Other than this, model parameters are set at their median values from Table 1,
 8 the surrounding vegetation has a height of 0 m and vertical wind speeds are set at 0 ms^{-1} .



9

1 **Figure 3.** The initial pitch resulting in maximum dispersal distance as a function of horizontal wind
2 speed and direction. Optimal pitches were found by a combination of golden section search followed
3 by a one-dimensional simplex algorithm (R functions optimise and optim; Brent, 1973, Nelder and
4 Mead, 1965). Roughness in the surface is caused by the optimisation routines and slight variation in
5 computed dispersal distances introduced by the fixed time step of numerical integration. As in Fig. 2
6 seeds were simulated with the median parameter values in Table 1 and with surrounding vegetation
7 height of 0 m and a vertical wind speed of 0 ms⁻¹.

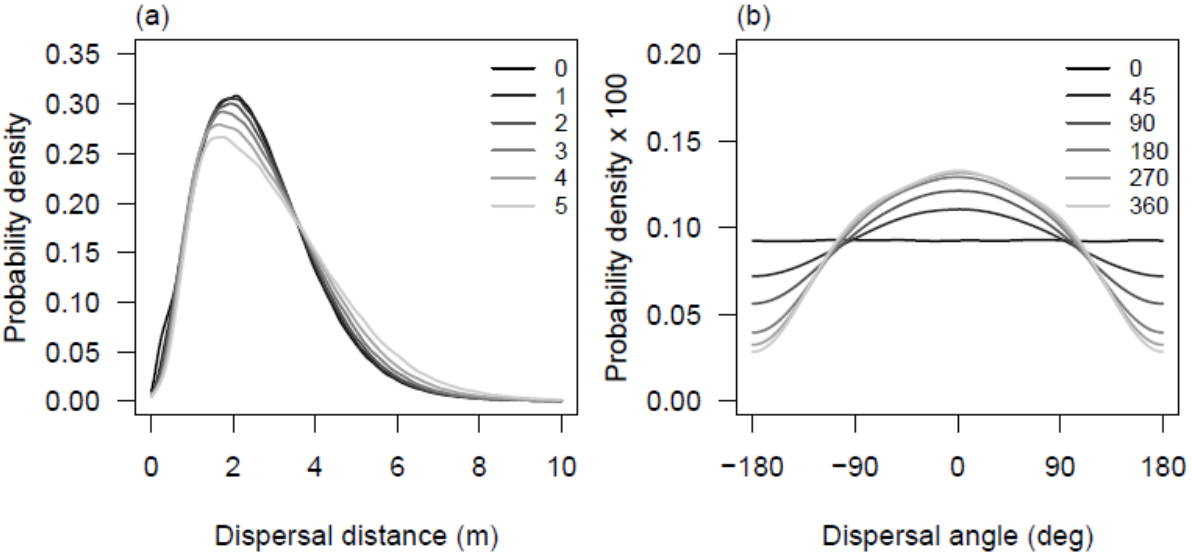


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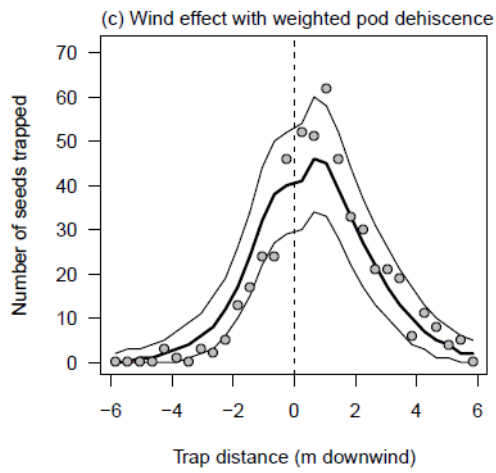
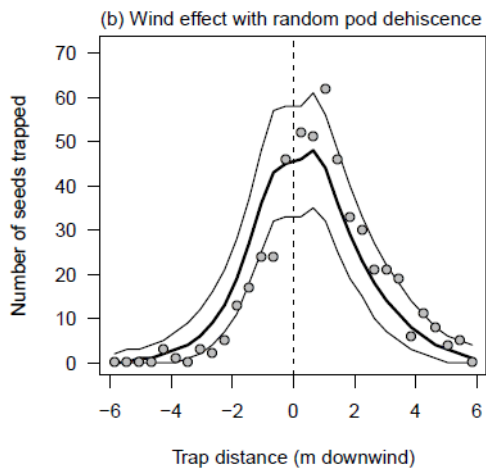
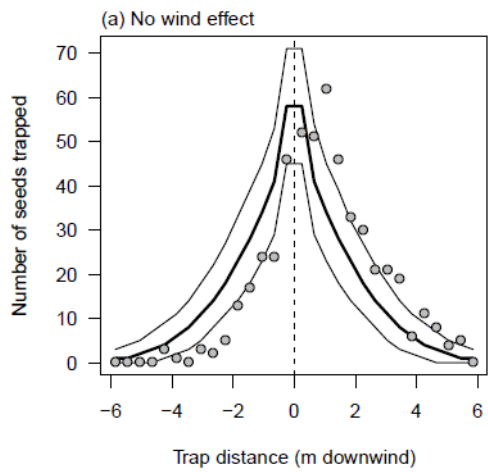
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Figure 4. Effects of wind characteristics on modelled seed dispersal patterns, produced by the neural network approximation to the mechanistic seed dispersal model. (a) Dispersal kernels (distributions of dispersal distances) produced by simulating 10^6 seeds released with horizontal wind velocities drawn from log-normal distributions of varying mean (line shading, ms^{-1} at 5 m height) and a standard deviation of 0.25 on the log-scale. (b) Distribution of dispersal directions in the horizontal plane, displayed as deviations from the direction of the prevailing wind. Seeds are released in a uniformly random direction, while wind directions are drawn from von Mises distributions with varying concentration parameters (line shading, deg), which is analogous to the inverse of a standard deviation. In (b) wind velocities follow a log-normal distribution with a mean velocity of 3 ms^{-1} . As the wind becomes increasingly directional so the seeds are increasingly dispersed in the direction it is blowing in.



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2 **Figure 5.** Comparison of observed data from the seed trapping experiment (points) with that
3 produced in 10000 simulations using the neural network approximation to the mechanistic dispersal
4 model. Model seeds were released with parameters drawn from the distributions in Table 1, except
5 that the seed pitches were based on the distribution of angles presented by X ripe pods in the
6 experiment, fitted as truncated Cauchy (location = 67.41, scale = 17.86, min = -90, max = 90). These
7 were used as the pods hung more vertically than those used in the video experiment in which seed
8 pitches were strongly correlated to pod angles ($r = 0.736$). Thick lines show the model medians,
9 while thin lines bound the 95th percentile ranges. In (a) the model ignores the effects of the wind on
10 seed dispersal. In (b) seeds are dispersed into a randomly chosen wind vector, while in (c) the
11 sampling of wind vectors is biased towards strong winds to represent an increased probability of
12 seed pod abscission. Traps were aligned in the direction of the prevailing wind. Downwind refers to
13 the direction relative to the prevailing wind rather than current wind.



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2 **Appendix S1. Neural network approximation to the seed dispersal model**

3 The seed dispersal model was formulated as a differential equation, which required numerical
4 integration to simulate the trajectory of *Impatiens glandulifera* seeds during ballistic dispersal (see
5 main text). The computational intensiveness of the procedure meant it was impractical to simulate
6 the millions of seed dispersal events needed for validating the model and estimating dispersal
7 kernels. Therefore we trained neural networks to predict dispersal distances and directions from the
8 seed parameters and wind conditions, and used this approximation in all subsequent model
9 simulations.

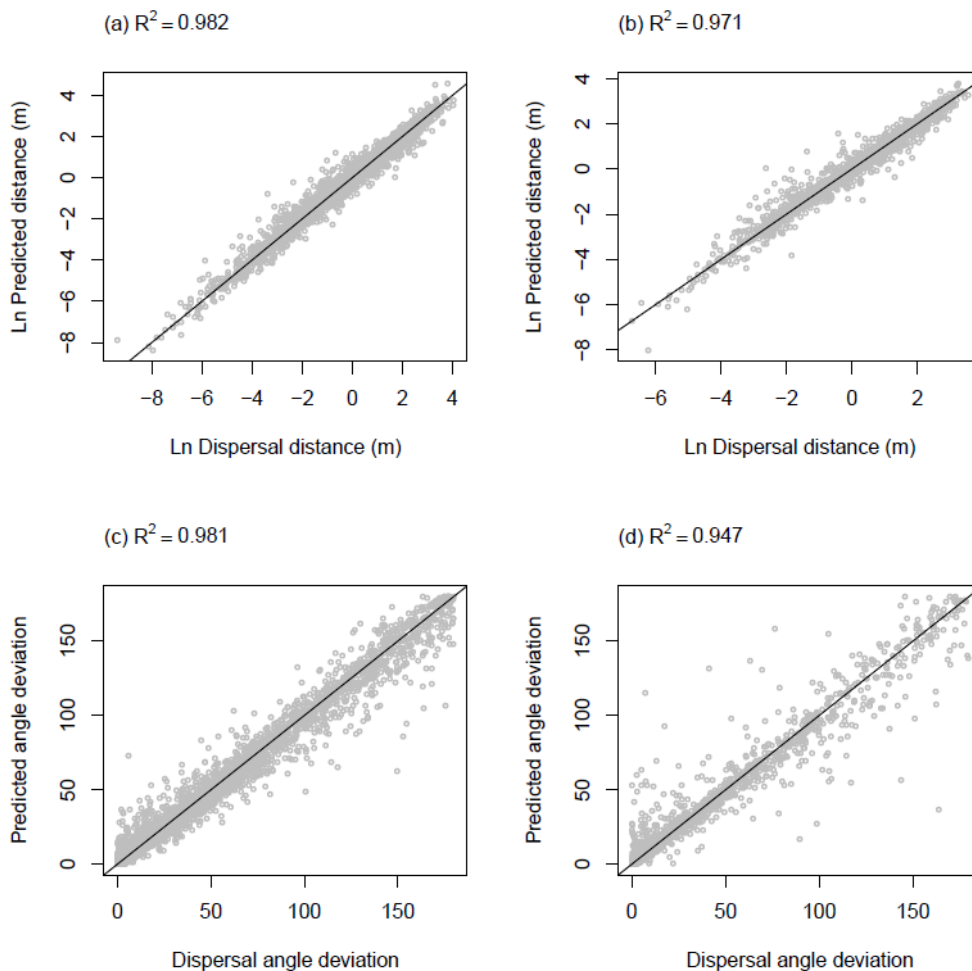
10 Single-hidden-layer neural networks with 40 hidden neurons, skip-layer connections and linear
11 output units (Bishop, 1985, Ripley, 1996) were fitted using the 'nnet' R package (Venables and
12 Ripley, 2002). To produce data to train the neural networks, 10000 dispersal events were simulated
13 with random parameter values uniformly distributed over the full range of recorded variation. This
14 dataset was then split randomly into a training partition of 7500 data points and testing partition of
15 the remaining 2500.

16 Prior to model fitting the following transformations were applied:

- 17 • Dispersal distances were natural log transformed. This improved their conformity to a Gaussian
18 distribution and ensured back-transformed predicted distances were always >0.
- 19 • Dispersal directions were converted into absolute deviations from the seed's initial direction (0-
20 180°). The deviation was then divided by 180° and arcsine-square root transformed, so that
21 back-transformed predicted deviations were always between 0 and 180°. The sign of the original
22 deviation was saved so that the predicted absolute deviation could be converted back into the
23 actual deviation.
- 24 • After any transformation, input variables were standardised on the range 0 to 1 to aid
25 convergence of the neural network training.

1 The input variables used to predict dispersal distances were seed mass, diameter, initial launch
 2 height above surrounding vegetation, initial velocity and pitch as well as the horizontal and vertical
 3 wind velocities at 2.5 m above ground and its horizontal direction. The same variables were used to
 4 predict dispersal angle deviations, and we also included (log-transformed) dispersal distance as a
 5 predictor. Both neural network models gave highly accurate predictions although in a very small
 6 number of cases dispersal directions were poorly predicted (Fig. S1).

7 **Figure S1.** Plots of (a-b) dispersal distances and (c-d) direction deviations produced by numerical
 8 integration of the full model against those predicted by the neural network approximations. Results
 9 for the training data partition are plotted in (a) and (c), while results for the testing partition are
 10 shown in (b) and (d). R^2 values are given as the squared Pearson's correlation coefficients and black
 11 lines show 1:1 correspondence.



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