Velocity of the falling dispersal units in *Zelkova abelicea*: remarkable evolutionary conservation within the relict tree genus

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PREMISE: Seed dispersal is extremely important for the recovery and restoration of forest communities. Relict tree genus *Zelkova* possesses a unique dispersal mechanism: mature fruits fall with the entire twig, and the dried leaves that are still attached function as a drag-enhancing appendage, carrying the fruits away from the parent tree. This singular adaptation has never been investigated in *Z. abelicea*.

METHODS: Drop tests with dispersal units and individual fruits of *Z. abelicea* were performed in controlled conditions to measure their dispersal velocity and to define their flight mode.

RESULTS: *Zelkova abelicea* uses both slowly falling dispersal units with chaotic motion, as well as fast falling individual fruits using a straight path. The falling velocity of *Z. abelicea* dispersal units is 1.53 m s^{-1}, which is virtually identical to that of the East Asiatic *Z. serrata* (1.51 m s^{-1}). In contrast, the falling velocity of individual fruits was 2.74 m s^{-1} (*Z. serrata*: 5.36 m s^{-1}).

CONCLUSIONS: Members of the genus *Zelkova*, growing today in distant regions, show remarkable evolutionary conservation of the velocity and flight mechanics of their dispersal units. This is surprising because the Mediterranean and East Asiatic *Zelkova* species have been separated at least 15–20 mya. *Zelkova abelicea*, although growing in the Mediterranean with completely different forest structure and composition, still uses the same dispersal mechanism. The dispersal capacity of the genus *Zelkova* is less efficient than that of other wind dispersed trees, and it presumably evolved for short-distance ecological spread and not for long-distance biogeographical dispersal.

KEY WORDS Crete; diaspore flight dynamics; relict tree; seed dispersal; terminal velocity; threatened species; Ulmaceae; wind dispersal.

Seed dispersal is universally considered extremely important for metapopulation dynamics and for the recovery and restoration of Mediterranean forest communities (Trakhtenbrot et al., 2005). Members of the relict tree genus *Zelkova* (Ulmaceae) possess a unique dispersal mechanism (referred sometimes as "decurtation"): mature fruits fall with the entire twig, and the dried leaves that are still attached function as a wing-like drag-enhancing appendage, carrying the fruits away from the parent tree (Kozlowski and Gratzfeld, 2013). The detachment of the fruiting shoot is not incidental but is related to the abscission process, similar to that of the autumnal shedding of leaves. However, nothing is known about the anatomy of the abscission zone. Generally, this singular adaptation of the genus *Zelkova* has been poorly studied (Hoshino, 1990;

Oyama et al., 2018b), and it has never been investigated in *Z. abelicea* (Kozlowski et al., 2018).

Relict tree species of *Zelkova* were important elements of the vast forests that prevailed throughout the Northern Hemisphere during much of the Cenozoic Period (Mai, 1995; Fineschi et al., 2002, 2004). Relicts are remnants of past populations that have become fragmented by climate-driven changes and habitat loss (Hampe and Jump, 2011). They were left behind during past range shifts and can persist today only in enclaves of benign environmental conditions within an inhospitable regional climate (Woolbright et al., 2014). Currently, the *Zelkova* genus comprises six extant species with disjunct distribution patterns (Wu and Raven, 2003; Denk and Grimm, 2005; Kozlowski et al., 2018): three in eastern Asia (*Z.*

serrata, *Z. schneideriana* and *Z. sinica*), one in southwestern Asia (*Z. carpinifolia*) and two on the Mediterranean islands of Sicily (*Z. sicula*) and Crete (*Z. abelicea*).

Zelkova abelicea (Lam.) Boiss. is a broadleaved endemic tree of Crete (Fazan et al., 2012) (Fig. 1). This species was supposedly widespread in the past and may have formed a forest belt in the Cretan Mountains (Søndergaard and Egli, 2006). It is currently found in scattered and isolated stands within the five main mountain ranges of Crete (Lefka Ori, Psiloritis, Kedros, Dikti, and Thripti) distributed from 900 m a.s.l. to the upper tree limit at approximately 1800 m a.s.l. (Egli, 1997; Kozlowski et al., 2014). In some areas, *Z. abelicea* may form mixed stands with *Acer sempervirens, Quercus*
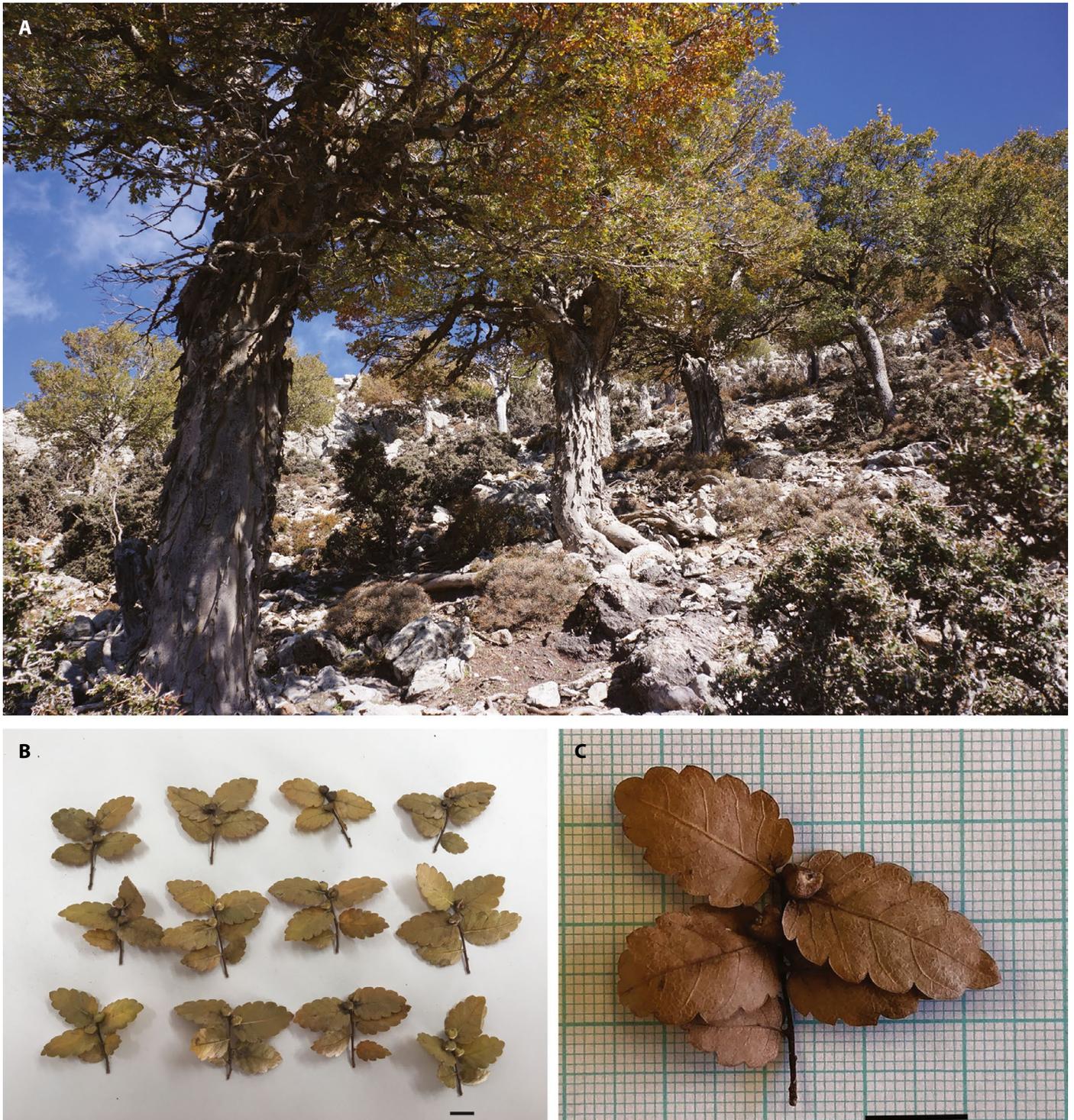
FIGURE 1. Dispersal units of *Zelkova abelicea*. (A) Population composed of large and fruiting trees (Dikti Mountains, Crete); (B–C) Closeup showing the morphology and variability of dispersal units used in this study. Scale bars = 10 mm.

coccifera, and occasionally *Cupressus sempervirens*. Most frequently, however, the species has a scattered distribution with few to no arborescent individuals in a more or less degraded phrygana with numerous dwarfed individuals.

The species does not tolerate very xeric conditions and is therefore preferentially found on north-facing slopes in and around dolines where the soil moisture and water supply are most adequate (Egli, 1997; Søndergaard and Egli, 2006). *Zelkova abelicea* is also found growing on scree slopes and around riverbeds that are active only during extreme precipitation events as well as at high elevations on south-facing slopes. It is most frequent in the Lefka Ori and Dikti Mountains, with only one known population in the Psiloritis and Thripti Mountains and a very scattered but widespread population on Mt. Kedros (Egli, 1997; Kozlowski et al., 2018). The species is listed as endangered in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Kozlowski et al., 2012), is protected under Greek law, and is included in the Bern Convention and in Annexes II and IV of the European Habitats Directive (Fournaraki and Thanos, 2006). Pastoral activities pose the most important threats to the species, as not only browsing by goats, but also trampling by numerous sheep or goats prevent seedlings from establishing and dwarfed shrubs from growing tall and fructifying.

The aim of our work was to understand the underlying fluid mechanics of *Z. abelicea* dispersal units. More specifically, we aimed to answer the following questions: (1) What is the falling velocity of the dispersal units in comparison with solitary fruits of *Z. abelicea*? (2) What is the velocity of the dispersal units of *Z. abelicea* in comparison with other *Zelkova* species and other wind dispersed plants? (3) What is the flight mode of the dispersal units? Finally, we discuss the implications of our findings to understand the ecology of *Z. abelicea* and the implications for conservation of this endangered relict tree.

MATERIALS AND METHODS

List of abbreviations used in this study

C_D: drag coefficient of dispersal unit, C_d: drag coefficient of individual fruit, d: diameter of seed, g: gravity acceleration, h: height of release, l: length of leaf, m: mass of dispersal unit or fruit, P: perimeter of the dispersal unit, Q: isoperimetric quotient ($Q = 4\pi S/P^2$), Re: Reynolds number ($Re = \rho w d/\mu$), S: surface area of dispersal unit, SA: surface area of fruit, t: leaf thickness, U_c: average wind velocity, W: weight ($W = mg$), w: terminal velocity, x_m: mean distance ($x_m = hU_c/w$), μ: air dynamic viscosity, ρ: air density, ψ: sphericity ($\psi = \pi d^2/SA$).

Dispersal units and their properties

Plant material (naturally detached dispersal units of *Z. abelicea*) was obtained from the Conservatory and Botanical Garden of Geneva (Switzerland). Randomly selected diaspores were used for further experiments and analyses at the University of Edinburgh (Fig. 1). The measurement techniques were done as described in Cummins et al. (2018). For each dispersal unit and fruit, we measured once per object (32 dispersal units, 27 fruits, and 126 leaves) the mass m using a Sartorius Extend balance (Sartorius Weighing Technology GmbH, Göttingen, Germany) with a standard deviation of 1 mg.

We considered the wing loading of the dispersal unit, defined as the ratio between its weight ($W = mg$, where $g = 9.81$ m s^{-2}) and the leaf surface area S. For the calculation of S, the dispersal units were placed over a flat surface, and the projected area on the horizontal plane was measured with a camera and the image processing software Fiji (Schindelin et al., 2012) (Fig. 1, Appendix S1). The length of leaves l was also measured as the maximum Euclidean distance between two points of the leaf. The leaf thickness t was evaluated with an RS PRO Micrometer External (RS Components Ltd., Corby, Northants, United Kingdom), with an accuracy of 1 μm.

Drop tests

The flight path and terminal velocity w of dispersal units and fruits alone were studied by performing drop tests. We used a similar experimental setup in the so-called "dead air space" as described in Oyama et al. (2018b) to avoid the influence of any air movement and to better compare both studies. This drop test took place in a closed room without windows and minimizing the movements, to reduce air motion. Testo 405 (Testo Ltd., Alton Hampshire, United Kingdom), a thermal anemometer, was used to ensure the presence of still air in the region of the experiment, according to Cummins et al. (2018) and Murren and Ellison (1998). Testo 405 was placed on a rod, more than 0.2 m from the vertical axis where the fruit was falling and far from the ground. Dispersal units ($n = 32$) and fruits removed from the dispersal units ($n = 27$) were dropped three times, with zero initial velocity from a height of 1.8 m in quiescent air, to record a complete fall over 1 m, at a distance of 1 m from the camera. The 95% confidence intervals were calculated using bias-corrected and accelerated bootstrapping.

The fall occurred in the focal plane of the camera at a distance greater than 200 mm from every solid boundary to avoid wall effects (Clift et al., 1978). A black background was used to facilitate the motion detection algorithm (Appendix S1 and S2). The camera recorded movies with a pixel size of 0.86 mm and a field of view of 1920 × 1080 pixels at 30 fps (Appendices S3–S6). An average of 17 frames recorded each drop test of the dispersal unit, while an average of seven frames recorded the drop test of the fruits. The difference in the number of frames is due to the different terminal velocities. A chessboard placed on the average sinking plane of the dispersal units allowed for the calibration of Tracker (Brown and Cox, 2009), the motion detection software. It allowed us to track dispersal units and fruits, as was also done in Cummins et al. (2018). Motion blur was not an issue. Dispersal units perform a chaotic motion, offering different sides to the camera during their fall; this was an issue and when it occurred, it was solved by manually selecting the dispersal unit. The instantaneous vertical velocities measured for each dispersal unit were confronted with the mean terminal velocity computed from the total time needed to fall 1 m (Vincent et al., 2016). The difference between the terminal velocities obtained with the two methods is on average lower than 1%.

Finally, for both fruits and dispersal units, we calculated the Reynolds number $Re = \rho w d/\mu$, where $d = 2l$, $\rho = 1.225$ kg m^{-3} is the air density, and $\mu = 1.81 \times 10^{-5}$ kg m^{-1} s^{-1} is the air dynamic viscosity. The Reynolds number is a nondimensional parameter that describes the relative importance of inertial to viscous forces in a fluid (air in this case).

The theoretical background used to analyze the fall of dispersal units is that of a falling disk (Field et al., 1997), influenced by its geometry (Esteban et al., 2018), which experiences four distinct types

of motion: steady falling, fluttering, chaotic, and tumbling (Field et al., 1997). "Steady-falling" motion: the object, dropped with any initial orientation, quickly settles down to a steady fall with a fixed orientation. "Fluttering" or periodic-oscillating motion: the object oscillates with a defined period, settling into this pattern after initial transient are damped. "Chaotic" motion: an object in this regime oscillates, flips over, and tumbles several times before suddenly jumping back to the oscillations. The number of tumbles and the direction of motion appear to be random. "Tumbling" motion: the object turns continuously end over end, while drifting in one direction.

A description of the geometry comes from the isoperimetric quotient $Q = 4\pi S/P^2$ (Esteban et al., 2018), where P is the perimeter of the dispersal unit. The isoperimetric inequality, $Q \leq 1$, highlights that Q decreases with a geometry departing from that of a circular shape because of the increase in P. The dispersal units have $Q = 0.32$ (0.30 – 0.34, 95% confidence interval), which is far from the values studied in the literature (Esteban et al., 2018). The dispersal units with an uneven mass distribution (seeds account for 30% of the mass), wavy edges, sharp corners, or rough and perforated surfaces (Moffatt, 2013) present a geometry that is difficult to model.

RESULTS

Falling velocity of dispersal units

The mean terminal velocity (of all of the instantaneous velocity measurements of all the dispersal units) of *Z. abelicea* was $w = 1.53$ m s^{-1} (1.44 m s^{-1} – 1.74 m s^{-1}, 95% confidence interval) (Table 1, Appendix S7), with a mass $m = 67.1$ mg (61.3 g – 73.5 g, 95% confidence interval). This terminal velocity, together with a mean length of the longest leaf in each dispersal unit $l = 18.94$ mm (18.31 mm – 19.81 mm, 95% confidence interval), gives a Reynolds number $Re = 3992$ (2654 < Re < 9052).

A flat disk perpendicular to the upcoming flow has a drag coefficient C_D of 1.18 (Fail et al., 1959), and C_D is a dimensionless quantity dictated by the shape. The terminal velocity is $w = \sqrt{2W/\rho S C_D} = 1.45$ ms^{-1}, which is close to the measured terminal velocity w of the dispersal unit reported in Table 1. Figure 2 shows that pappose seeds, spinning winged seeds, and gliding seeds, such as those of *Alsomitra macrocarpa* taken from Minami and Azuma (2003) and Lentink et al. (2009), when performing a steady flight, are grouped away from *Z. abelicea* in the parameter space linking wing loading (W/S) and terminal velocity (w). These wind-dispersed fruits perform their flight at a lower wing loading, and thus, *Z. abelicea* is a rather weak disperser.

Falling velocity of an individual fruit

The mean velocity for the detached individual fruits of *Z. abelicea* was $w = 2.74$ m s^{-1} (2.70 m s^{-1} – 2.78 m s^{-1}, 95% confidence interval)

(Table 1, Appendix S8). The *Z. abelicea* fruits present a nonspherical shape with a diameter $d = 2.92$ mm (2.82 mm – 3.03 mm, 95% confidence interval) and a mass $m = 10.6$ mg (10.0 mg – 11.1 mg, 95% confidence interval). Fruits account for almost one third of the mass of a dispersal unit. The size coupled with a terminal velocity gives an $Re = 541$ (521 < Re < 564). Within this Reynolds number range, Haider and Levenspiel (1989) provide a curve-fit equation for the drag coefficient on nonspherical particles:

$$C_d = (24/Re)\left(1 + C_1 Re^{C_2}\right) + C_3 / \left(1 + C_4/Re\right),$$

$$C_1 = \exp\left(2.33 - 6.46\psi + 2.45\psi^2\right),$$

$$C_2 = 0.096 + 0.556\psi,$$

$$C_3 = \exp\left(4.90 - 13.89\psi + 18.42\psi^2 - 10.26\psi^3\right),$$

$$C_4 = \exp\left(1.47 + 12.26\psi - 20.73\psi^2 - 15.89\psi^3\right).$$

Sphericity ψ is the ratio of the surface area of a sphere with the same volume as the particle to the surface area of the particle SA, the fruit in this case,

$$\psi = \frac{\pi d^2}{SA}.$$

The sphericity is 1 for spheres and decreases as the particle becomes less spherical. A best fit of $C_d = 3.40$ (2.48 < C_d < 4.63) and Re values for every fruit gives a sphericity $\psi = 0.56$ (0.54 – 0.59, 95% confidence interval).

### Dynamics of a falling fruit and a dispersal unit

The falling fruits without twigs and leaves move in a straight and steady path (Appendices S2, S3, and S6). The sinking path of dispersal units with attached fruits is two dimensional and "chaotic" (according to the terminology of Vincent et al., 2016). The horizontal distance reached by the dispersal units, dropped three times from a height of 1.8 m, is shown in Fig. 3. These distances are normally distributed with a peak of 27 mm from the source plant. All dispersal units analyzed fell in a radius less than 332 mm from the point of release. A ballistic model gives

$$x_m = h\frac{U_c}{w},$$

where x_m is the mean distance that a dispersal unit will cover when a given height of release h and average wind velocity U_c (Murren and Ellison, 1998) is applied. A tree of *Z. abelicea* 20 m in height (in good ecological conditions and without livestock browsing on Crete, Kozlowski et al. [2014]) and exposed to a wind speed of 10 m

TABLE 1. *Zelkova abelicea* diaspores (individual fruits and dispersal units), their dimensions and flight characteristics.

		Mass	Leaf thickness	Diameter	Surface	Terminal velocity	Reynolds number
		m [mg]	t [mm]	d [mm]	S [mm²]	w [m/s]	Re
Dispersal unit	Mean	67.1	0.197	37.88	454.6	1.53	3992
	CI	61.3 – 73.5	0.192 – 0.205	36.62 – 39.62	413.3 – 503.2	1.44 – 1.74	2654 – 9052
Fruit	Mean	10.6	—	2.92	6.70	2.74	541.2
	CI	10.0 – 11.1	—	2.82 – 3.03	6.30 – 7.30	2.70 – 2.78	520.9 – 563.6
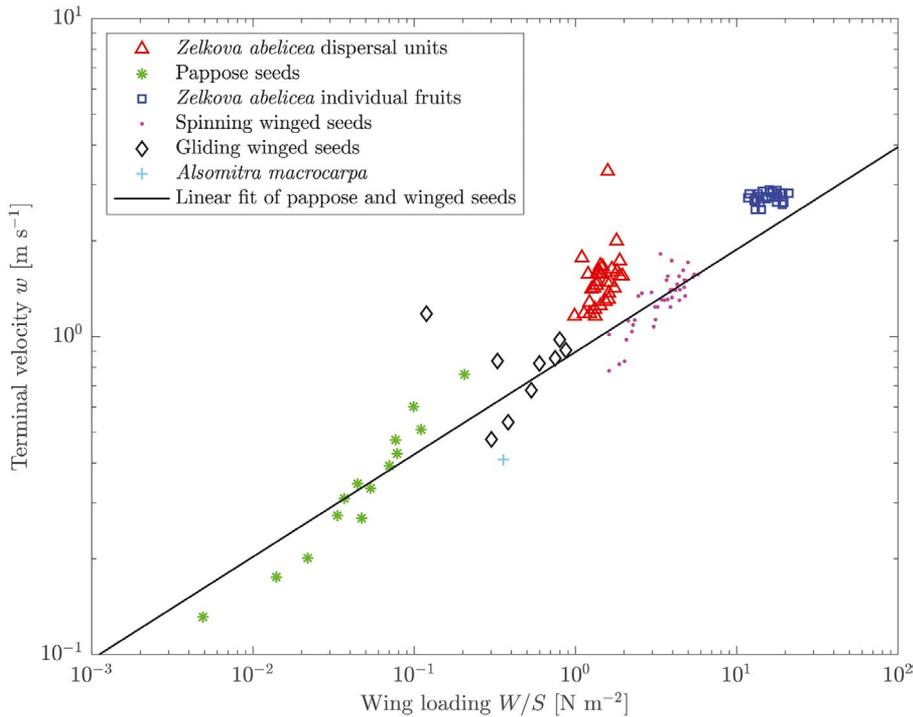
FIGURE 2. Terminal velocity versus wing loading for various seeds. The solid line shows the linear fit of all pappose and winged seeds, excluding *Z. abelicea*. Pappose seed data are taken from Minami and Azuma (2003), while spinning and gliding winged seed and *Alsomitra macrocarpa* (Cucurbitaceae) data are taken from Lentink et al. (2009).

s^{-1} could disperse fruits over an area of 130.7 m in radius. For heavy dispersal units, with $w > 1$ m s^{-1}, turbulence has a negligible effect on terminal velocity, and the ballistic model gives an accurate prediction of x_m (Murren and Ellison, 1998). The flight behavior changes with the number of leaves attached to a dispersal unit, affecting the results in terms of flight path and terminal velocity (Appendix S9). The chaotic motion described during the fall was plotted for all the dispersal units (plot example in Appendix S10, picture in

FIGURE 3. Distribution of the horizontal distance travelled by dispersal units over a 1-m fall.

Appendix S2, movies in Appendices S3 and S4). This chaotic motion gives a different flight path every time a dispersal unit falls in calm air.

A positive correlation emerged between the number of fruits and the mass of the dispersal units (Appendix S9). Fruits account for almost 30% of the mass of a dispersal unit (Appendix S11) and are the main contribute to an uneven mass distribution. A higher number of fruits is also related to a higher terminal velocity (Appendix S9), which, according to the ballistic model, translates into a shorter mean distance x_m. We also found that the number of leaves is positively correlated with the number of fruits and with the mass, but neither with the surface nor with the terminal velocity (Appendix S9).

DISCUSSION

Plants evolved very diverse dispersal units with often complex structures to facilitate movement via biotic or abiotic vectors (Seale and Nakayama, 2020). Along with animal, water, or explosive dispersal, wind is one of the most common carriers of fruits or seeds (Minami and Azuma, 2003; Cummins et al., 2018). Our results clearly demonstrate the flying capacities of the *Z. abelicea* dispersal units. Although less efficient than those of the other wind-dispersed trees, such as *Acer* (0.60–1.00 m s^{-1}) or *Liquidambar* (1.20 m s^{-1}), the velocity is lower than that of *Fraxinus* (1.60 m s^{-1}) (Green, 1980; Johnson, 1988; Hoshino, 1990). Leaves attached to the twig provide more than six times the amount of drag experienced by the individual fruit. Furthermore, under natural conditions, especially on steep slopes and in mountains, where *Z. abelicea* often grows (Kozlowski et al., 2014), updrafts and gusts will additionally increase the flying capacities and dispersal distance (Tackenberg et al., 2003; Oyama et al., 2018a). The dispersal units of *Z. abelicea* display an important variation in number of leaves and fruits attached to them during the dispersal (Appendices S7, S9). Interestingly, the number of fruits is more important for the dispersal distance (units with many fruits are heavier and fly at shorter distances) than the number of leaves. Although a larger number of leaves provides more surface for the drag forces, it enhances the weight of the whole dispersal unit. This differentiated structure of dispersal units might be an adaptation to disperse at different distances and thus covering various habitat patches around the mother tree. Moreover, we detected a chaotic motion of falling dispersal units of *Z. abelicea*, conversely to the straight path of individual fruits. Our results confirm that *Z. abelicea*, growing in the Mediterranean, possesses very similar dispersal behavior as their East Asiatic relatives (Oyama et al., 2018a). The dispersal capacity of the second Mediterranean species of the genus, *Z. sicula* from Sicily, has never been studied, mainly because of the rare fruiting of this tree (Garfi, 1997; Garfi et al., 2011).
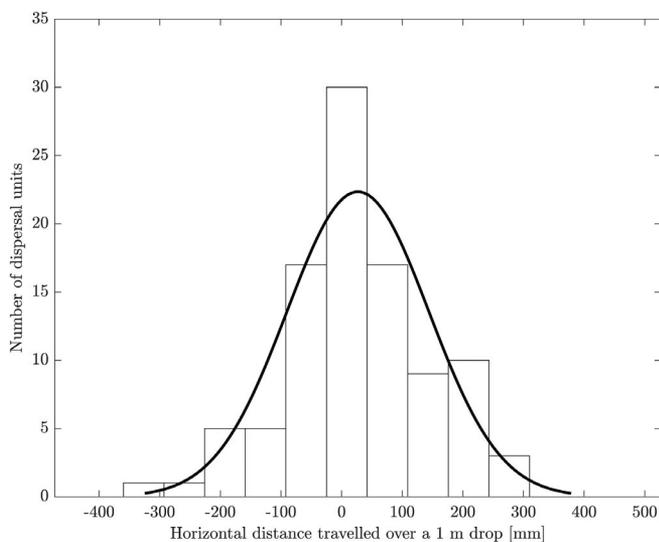
More interestingly however, our study shows that the falling velocity of dispersal units of *Z. abelicea* is virtually the same as in the East Asiatic counterpart *Z. serrata*, which is slightly above 1.5 m s⁻¹ for both species (Hoshino, 1990; Oyama et al., 2018b). The genus *Zelkova* probably evolved in the humid northern Pacific area of Eastern Asia and later became a very common component of temperate and subtropical forests across the whole Northern Hemisphere (Kozlowski et al., 2018). The Mediterranean and East Asiatic *Zelkova* species were separated at least 15–20 mya due to dramatic climatic changes in Central Asia and currently occupy very different regions and habitats (Christe et al., 2014; Kozlowski et al., 2018). Thus, members of the relict tree genus *Zelkova*, growing today in disjunct and very distant regions of Eurasia, show remarkable conservatism of the velocity and flight mechanisms of their dispersal units. The use of the same dispersal mechanism is somewhat surprising, because the relict tree *Z. abelicea* has been "imprisoned" for millions of years in the Mediterranean climate, dwelling in habitats with completely different forest structures and compositions (Fazan et al., 2012; Kozlowski et al., 2014). The independent development of such strong similarities in dispersal mechanisms is rather improbable. The rich fossil record shows the presence of abscissed dispersal units already very early in the evolution of the genus (Denk et al., 2017). In fact, the oldest known fossils of the genus *Zelkova* are fossilized dispersal units with attached fruits from the Oligocene period, found both in Europe (Manchester, 1989) and in China (Ma et al., 2017).

Furthermore, *Z. abelicea* shows a similarly variable flight behavior as detected by Hoshino (1990) and Oyama et al. (2018a) for *Z. serrata* in Eastern Asia; the Mediterranean species also uses both slowly falling dispersal units with chaotic motion, as well as fast falling individual fruits using steady falling. Oyama et al. (2018a) proposed that this strategy of using variable dispersal methods might be advantageous for establishment in a wide range of habitats within spatially heterogeneous environments. According to their study, which was carried out in *Z. serrata* forests in Japan, dispersal units can carry fruits far from adults (>30 m), mainly facilitating recruitment on steep slopes, whereas abundant individually detached fruits are disseminated beneath adults, enhancing seedling establishment in a wide range of slope inclinations. The complex topology of Crete and the existence of vigorous forest fragments of *Z. abelicea* on slopes make this variable dispersal strategy plausible for the Cretan endemic (Kozlowski et al., 2014). This may in fact explain why this variable dispersal mechanism was maintained despite the dramatic climatic and forest composition changes in the Mediterranean during the last million years.

In addition to the wind-dispersal capacities of *Zelkova* fruits, nearly nothing is known about the other potential dispersal vectors in this genus. Some authors observed sporadically that zoochory might also play a role in the fruit dispersal of *Z. abelicea*, notably with short-distance fruit transportation by ants (Egli, 1997; Kozlowski et al., 2018). In Eastern Asia, tree-dwelling mammals feed on and potentially disperse fruits of *Zelkova* species (Kozlowski and Gratzfeld, 2013). It was shown in many regions of China that *Zelkova* fruits (e.g., *Z. sinica* and *Z. schneideriana*) are one of the principal autumnal and winter foods for rhesus macaques (*Macaca mulatta*) (Lu et al., 2002; Guo et al., 2011).

More generally, however, and on a large geographical scale, *Zelkova* species possess restricted dispersal capacities. The dispersal capacity of *Z. abelicea* detected in our study presumably evolved, as discussed above, for short-distance spread within a population and/ or restricted area and not for long-distance biogeographical dispersal. Once long-distance disjunctions are formed, such as large water, edaphic (deserts) or orographic barriers, they are not conquerable by *Zelkova* species. Molecular work on genetic differences between *Z. abelicea* populations on Crete confirms extremely weak (or nonexistent) long-distance dispersal of this species (Christe et al., 2014). Notably, populations inhabiting each of the Cretan mountain chains (separated by a distance of 50–100 km) possess a unique genetic pattern, indicating no genetic exchange for several million years (Kozlowski et al., 2014, 2018). A similar pattern was found in *Z. carpinifolia* in Transcaucasia. Christe et al. (2014) demonstrated a large gap between two haplotype clusters: the first of the Hyrcanian region (Talysh and Alborz Mountains) and the second of the Colchic region (western Georgia and northeastern Turkey). Both disjunct population complexes (separated by a dry and forest-free gap) show very strong genetic differentiation, indicating no gene flow for several million years and thus no long-distance fruit dispersal (Christe et al., 2014).

Similar conclusions can be drawn from the fossil record of the genus *Zelkova* in Europe (Magri et al., 2017). *Zelkova abelicea* presumably arrived on Crete many millions of years ago, when the island was still connected with neighboring land masses via vast land bridges (Kozlowski et al., 2014). The last known occurrences of *Zelkova* in continental Europe still existed ~30 kya in Italy and ~120 kya in Greece (Follieri et al., 1986, 1998; Magri et al., 2017). However, the taxon went extinct there definitively during the last glacial period and survived only on isolated Mediterranean islands. The recolonization of Europe by the relict *Z. abelicea* from Crete will thus never happen via natural dispersal.

AUTHOR CONTRIBUTIONS

G.K. conceived the study. G.K., N.N., I.M.V., and D.C. designed the experiments, and D.C. conducted all experiments and data analyses. G.K. and D.C. both led the writing of the manuscript. L.F., N.N., and I.M.V. contributed to the interpretation of the results and to the writing and editing of the manuscript.

SUPPORTING INFORMATION

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

APPENDIX S1. Experimental setup used for the drop tests.

APPENDIX S2. Example of trajectories of a falling dispersal unit (A) and of a falling individual fruit (B), obtained by imaging from the side using the camera. The digitized images were processed with Tracker. Chaotic motion is detected for the dispersal units, while the fruit falls in a steady straight trajectory.

APPENDIX S3. Real-time video of falling dispersal unit.

APPENDIX S4. Slow-motion video of falling dispersal unit.

APPENDIX S5. Real-time video of falling single fruit.

APPENDIX S6. Slow-motion video of falling single fruit.

APPENDIX S7. Principal dimensions, terminal velocity, and type of motion of the dispersal units of *Zelkova abelicea*.

APPENDIX S8. Principal dimensions, terminal velocity and type of motion of the individual fruits of *Zelkova abelicea*.

APPENDIX S9. (A) Distribution of the number of fruits per dispersal unit. (B) Distribution of the number of leaves per dispersal unit. (C) Relationship between mass and number of fruits of the dispersal unit. (D) Relationship between mass and number of leaves of the dispersal unit. (E) Relationship between surface and number of leaves of the dispersal unit. (F) Terminal velocity versus wing loading for *Zelkova abelicea* dispersal units. The solid regression line represents the linear relationship. (G) List of correlation coefficients ($p < 0.05$). Box-plots: the 25th and 75th percentiles of the samples are top and bottom of each box, which thus includes the interquartile range. The horizontal line inside each box shows the median. Whiskers join the box with the furthest observations. Outliers, which are represented with a red cross, are observations more than 1.5 times the interquartile range away from the top or bottom of the box.

APPENDIX S10. Example of flight path measurements. Flight paths of all the dispersal units plotted on a plane, where the *x*-axis is the horizontal displacement and the *y*-axis is the vertical displacement. The different symbols highlight the location of the dispersal unit at each frame.

APPENDIX S11. Calculation of the proportion of the fruit mass in comparison with the whole dispersal unit (based on 15 selected dispersal units). Dispersal units have an average mass of 71 mg and present an average of two fruits each. The average mass of the fruits is 10 mg, hence they account for 28% of the mass of a dispersal unit.

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