Secondary dispersal mechanisms of winged seeds: a review

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Abstract

Winged seeds, or samaras, are believed to promote the long-distance dispersal and invasive potential of wind-dispersed trees, but the full dispersive potential of these seeds has not been well characterised. Previous research on the ecology of winged seeds has largely focussed on the initial abscission and primary dispersal of the samara, despite it being known that the primary wind dispersal of samaras often covers short distances, with only rare escapes to longer distance dispersal. Secondary dispersal, or the movement of the seeds from the initial dispersal area to the site of its germination, has been largely ignored - despite offering a likely important mechanism for the dispersal of samaras to microhabitats ideal for establishment. In this review, we have synthesised what is known on the predation and secondary dispersal of winged seeds by multiple dispersive vectors, highlighting gaps in the knowledge and offering suggestions for future research. Both hydrochory and zoochory offer the chance for samaroid seeds to more regularly disperse longer distances than anemochory alone, but the effects of the wing structure on these dispersal mechanisms has not yet been well characterised. Furthermore, although some studies have investigated secondary dispersal in samaroid species, the studies are scarce and only rarely track seeds from source to seedling. Future research must be directed to studying the secondary dispersal of samaras by various vectors, in order to fully elucidate the invasive and colonisation potential of samaroid trees.

Keywords: secondary dispersal, samara, anemochory, winged seed, diplochory

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40 *Introduction*

41 A samara is a dry, indehiscent fruit (or achene) containing one seed encompassed by a wing.
42 Samaras are adapted to wind dispersal in seasonally dry tropical ecosystems as well as
43 temperate regions prior to leaves opening (Mirle and Burnham, 1999). During samara
44 development, abscission layers develop which eventually allow for the release of the samara
45 under the right meteorological conditions (Bohrer *et al.*, 2008). Much research effort has been
46 directed toward understanding the dynamics of abscission and flight, but the subsequent fate
47 of seeds has been much less studied. Specifically, secondary dispersal, by wind, water, or
48 animal vectors, has received minimal attention (Vander Wall, 1992), and the influence of
49 samaras on seed predation and seed burial and germination have been similarly neglected.

50 Samaroid seeds are found in many unrelated taxa (Mirle and Burnham, 1999; Manchester and
51 O'Leary, 2010). They include highly invasive species, like *Ailanthus altissima* (Mill.) Swingle
52 (Kowarik and Säumel, 2008) and *Acer platanoides* L. (Säumel and Kowarik, 2010) which
53 currently threaten many native habitats across Europe and North America, as well as
54 economically important species like *Fraxinus excelsior* L., which is currently under threat of
55 extinction from ash dieback (*Hymenoscyphus fraxineus* Baral) (Coker *et al.*, 2019).
56 Understanding how the dispersive structure affects dispersal in these species is critical for our
57 understanding of their spread and survival, and yet very little research has been carried out.
58 Furthermore, species bearing winged seeds, despite often showing low initial dispersal
59 distances (Venturas, Nanos and Gil, 2014), appear to dominate early successional stages after
60 catastrophic disturbances like avalanches or volcanic eruptions (del Moral and Wood, 1993;
61 Nakashizuka *et al.*, 1993). Our knowledge of how the samara structure influences long-distance
62 dispersal, especially, would greatly improve our understanding of population dynamics,
63 changes in geographic range, invasions, and responses to changes in habitat and climate (Horn,
64 Nathan and Kaplan, 2001).

65 Seed fate is difficult to track, as the path from seed to seedling can involve numerous steps -
66 with mortality occurring at every phase (Figure 1). Long distance dispersal is especially
67 difficult to follow, as the larger sampling range is much more logistically challenging and
68 makes it a lot easier to miss rare dispersive and germination events. However, if we want to
69 know the full dispersive potential of a species it is critical that we learn the range of their
70 dispersal. As environments and climatic ranges rapidly change through human actions,
71 knowing the ability of species to maintain their range, colonise new locations, or invade
72 vulnerable habitats will be critical. Primary dispersal may act independently of secondary
73 dispersal, thus both processes must be understood in order to fully discover the seeds' potential.

74 There are three dominant mechanisms for variability in dispersal distance in plants (Higgins,
75 Nathan and Cain, 2003). The first mechanism states that exceptional behaviour of the most
76 common vector, for example, particularly strong updrafts (Nathan *et al.*, 2002), can cause long-
77 distance dispersal to occur. The second mechanism states that between-seed variability in
78 dispersal distances is primarily a property of the dispersal unit, for example that seeds (even
79 from the same parent) vary in mass and seed mass influences dispersal distance (Delgado,
80 Jimenez and Gomez, 2009). The last mechanism of long-distance dispersal of a fraction of
81 seeds involves the use of a nonstandard dispersal vector, for example a rodent caching a
82 primarily wind-dispersed seed (Vander Wall, 1994). This last mechanism often acts in
83 secondary dispersal.

84 Phase I, or primary, dispersal involves the movement of the seed from the parent plant to a
85 surface – often the ground beneath or near the parent (Chambers and MacMahon, 1994). Many
86 mathematical models have been constructed to predict the primary dispersal of samaras,
87 including models linking samara morphology to descent velocity (a frequently used substitute
88 for dispersal distance) (Planchuelo *et al.*, 2017), predicting the minimal wind speed required
89 for abscission (Bohrer *et al.*, 2008), predicting the relationship between seed mass and dispersal

distance (Greene and Johnson, 1993), and predicting the effect of canopy foliage on seed dispersal (Nathan and Katul, 2005). The initial seed dispersal creates a 'seed shadow', with most seeds located close to the parent plant and density tapering off as distance from the parent plant increases (Bontemps, Klein and Oddou-Muratorio, 2013). However, although the initial dispersal appears optimised to minimise seed predation and/or seedling establishment close to the parent plant (Bontemps *et al.*, 2013), the initial dispersal distance of winged seeds tends to be short (Venturas *et al.*, 2014), and even when long-distance dispersal occurs at this stage it may not necessarily lead to establishment if the microsite in which the seed is deposited is not favourable to germination (Nathan *et al.*, 2002). Secondary dispersal is likely an important driver of the spatial patterns seen in plant populations, influencing the risk of seed predation and distribution of microhabitats in which seeds lodge and can germinate, as well as influencing dispersal distances and directions (Chambers and MacMahon, 1994).

Although it is known that the initial dispersal of most samaras is generally less than 30 metres (Venturas *et al.*, 2014) very little attention has been given to the secondary, or phase II, dispersal of samaras. Tracking individual seeds may be difficult, but it is well known that wind-dispersed plants can colonise over large distances (order of magnitude more than 30m). Samaras that are uplifted to travel long distances under their initial dispersal tend to be lighter, and worse competitors as seedlings (Nathan *et al.*, 2002), thus secondary, or phase II dispersal may be an important contributor to the establishment of individuals at longer distances away from the parent. However, secondary dispersal does not necessarily follow the same dispersal mechanism as the primary dispersal. Diplochory, or seed dispersal by a sequence of different dispersal agents, is likely to be responsible for a substantial proportion of long-distance dispersal events (Vander Wall and Longland, 2004).

Furthermore, there is little evidence in the literature on samaras of research on the effect of wing structures on diplochory, or the speed of degradation and the subsequent effect of wing

removal on the appeal of samara-seeds to animals. If diplochory increases the chances of seedling establishment or overall plant fitness, selection can be expected to act on samara structures to increase the chances of secondary dispersal. This could mean that selection would favour greater wing surface area, so that the flotation ability of the seed is improved (Säumel and Kowarik, 2013), or that the seed and wing separate faster in species that use animal as well as wind dispersal in order to decrease the energetic cost of seed predation. For example, in the species *Ailanthus altissima*, it has been reported that samaras with slower descent velocities also have longer floating times in water (Planchuelo, Catalán and Delgado, 2016).

As the field has thus-far largely ignored the potential of diplochory in wind-dispersed seeds (except, perhaps, for pine-seeds which are well known to be collected by rodents (Vander Wall, 1992)), future research should focus on determining the full range of dispersal distances of samaras, and the various methods by which they might travel, as well as which dispersal methods provide the best opportunities for establishment. These topics could be integral to future discussions regarding the ability of samara-bearing trees to adapt to the changing climatic boundaries, or their ability to recover and recolonise following traumatic climate events.

Furthermore, the evolutionary history of diplochoric species could be unravelled to determine how diplochory came about, and what the ancestral methods of dispersal may have been. This would allow us to elucidate the selective effect of different modes of dispersal on samara structure. When we understand how samara traits influence secondary dispersal, we can combine that with our (currently much more advanced) understanding of how these traits influence primary dispersal in order to explore to what extent (if any) samara traits are selected to enhance secondary dispersal and what the consequences of this for primary dispersal might be. Conversely, we can also better understand how selection for airborne primary dispersal influences secondary dispersal. This approach very much mirrors the recommendations of

140 Saatkamp *et al.* (2019) who called for the development of a seed-trait functional ecology that
141 extends beyond seed mass. Specifically, they call for research on the selective consequences
142 of seed traits to extend beyond the current strong focus on seed mass. Samaras are a very natural
143 focus for such endeavour because there will be subtle interplay between traits of the seed (most
144 obviously its mass) and traits of the samara that encapsulates it – and a better understanding of
145 samara traits is essential for gaining a predictive ability of seed fate.

146

147

148 *(1) Samara morphology and primary dispersal*

149 Samara-bearing species are found on every continent except Antarctica in habitats including
150 deserts, rainforests, temperate, and alpine regions. Growth forms bearing samaras include trees,
151 vines, shrubs, and herbs. The taxonomic diversity of samaras is still tenuous, although an
152 assimilation of data by Manchester and O'Leary (2010) found more than 140 genera spread
153 across 45 families and 25 orders that contained species bearing winged seeds. Fossil records of
154 samaroid seeds date back to the early Cretaceous, and fossils have been classified to belong to
155 separate and unrelated families even then (Manchester and O'Leary, 2010). Among the species
156 that use samaras for dispersal are several economically important genera including *Fraxinus*
157 L. and *Pinus* L., as well as highly invasive species like *Ailanthus altissima, Acer ginalla*
158 Maxim., *A. platanoides*, and *Tachigalia versicolor* Standl. and L.O. Williams.

159 Although there has been convergent evolution in the development of samaras (Manchester and
160 O'Leary, 2010), samara structures still show differences both between and within species (Sipe
161 and Linnerooth, 1995). The differences in samara structure are partially due to evolutionary
162 constraints. Samara wings are thought to develop from either the style or the ovary wall (Mirle
163 and Burnham, 1999) and the wing number appears to reflect the number of carpels found in

the species (Manchester and O'Leary, 2010). Wing venation, on the other hand, appears to reflect the tissues the wing derives from (Manchester and O'Leary, 2010).

Samaras are usually separated into two categories: "rolling" and "non-rolling", where "rolling samaras" autogyrate as well as autorotate, while "non-rolling samaras" only autogyrate (Figure 2) (Augspurger, 1986). "Rolling samaras" are usually symmetrical, like the samaras of *Fraxinus* sp. while "non-rolling samaras" tend to be asymmetrical like the samaras of *Acer* sp. "Rolling samaras" are known to have a faster rate of descent, although the relationship between wing loading and terminal velocity is identical for both types of samaras, and only differ by a constant (Green, 1980). The potential dispersal distance of a samara is thought to be inversely related to their rate of descent, thus predicting that "non-rolling samaras" will travel farther on their initial dispersal (Augspurger, 1986).

Samara morphology is most likely convergent due to flight constraints, as shown by Augspurger (1986), who found that wing loading values are similar across species despite differences in seed mass and area over six orders of magnitude (0.0194 – 3055mg and 0.0029 – 155cm^2, for the species *Macrocnemum glabrescens* Benth. and *Cavanillesia platanifolia* (Humb. And Bonpl.) Kunth respectively). However, despite wing loading constraints, samara shape and mass differ both between and within species, as well as within individuals. It should be self-apparent that, if two samaras with identical mass and wing area have different shape or mass distributions they will fly differently (Sipe and Linnerooth, 1995). Why then, do individual trees produce such varying propagules rather than strongly converging on an optimum?

Greene and Johnson (1993) argue that dispersal capacity may be a compromise, rather than an optimum, as the fruit has a purpose beyond dispersal. Seed mass is thought to be inversely related to dispersal ability, while seed mass appears to be proportional to establishment

188 potential, although this is mediated by environmental conditions (Delgado *et al.*, 2009). This
189 trade-off between dispersal ability and maternal provisioning of the seed must be present, and
190 in turn suggests that seed size is inversely correlated to parental fecundity but positively
191 correlated with seedling survival (Harper 1977, in Greene and Johnson, 1993). Interspecifically
192 Augspurger (1986) provided a detailed catalogue that suggests that wing-loading of samaras
193 can vary between 1,346.89 and 68,486.89 millidynes cm^{-2}, for the species *Jacaranda copaia*
194 (Aubl.) D. Don and *Platypodium elegans* Vogel, respectively. Crucially, however, (Greene and
195 Johnson, 1992a) demonstrated both empirically and theoretically that this variation had a trivial
196 effect on primary dispersal distance compared to likely variation in wind characteristics at the
197 point of abscission from the parent.

198 The variability in samara seed size does appears to influence the dispersive potential of seeds
199 and the probability of seedling survival (Delgado *et al.*, 2009), although it should be noted that
200 the relationship between dispersal and seed size has only been found in samaroid seeds. Other
201 wind dispersed seeds, like plumed or parachute seeds, do not appear to show the same
202 relationship (Greene and Johnson, 1993). In samaroid species, the general trend seems to be
203 that lighter seeds tend to travel further, while heavier seeds produce more competitive seedlings
204 (Nathan *et al.*, 2002), although some studies appear to refute this (Landenberger, Kota and
205 McGraw, 2007; Delgado *et al.*, 2009).

206 Most wind-dispersed seeds appear to be designed to be released under optimal dispersal
207 conditions, and it is known that seed abscission is only effective under certain wind conditions,
208 if dispersal is to occur (Bohrer *et al.*, 2008). Abscission in most samara-bearing species occurs
209 due to drag forces which act in the direction of the airflow (Bohrer *et al.*, 2008). Higher long-
210 distance dispersal potential is more frequently associated with high-speed horizontal winds,
211 although abscission itself increases with the prevalence of vertical updrafts (Greene and
212 Johnson, 1992b; Maurer *et al.*, 2013). The seed formation itself also appears to be adapted for

release under high wind conditions. *Liriodendron tulipifera* L. seeds release first on the inside of the seed cluster, thus staying caught in their sibling-seeds until wind jostles the branches (Horn *et al.*, 2001). *Fraxinus americana* L. only releases its seeds under high wind conditions, most likely due to the development of the abscission layer (Horn *et al.*, 2001).

Abscission occurs only after the separation layers have formed (Greene and Johnson, 1992b), which break under strong wind conditions when the wind direction causes the drag force exerted to pull the seed away from the plant (Savage, Borger and Renton, 2014). Seeds are released more easily during faster winds, and multi-directional wind may aid in loosening the samara stem, thus increasing the release magnitude (Savage *et al.*, 2014). The abscission layers form faster under less humid conditions, and if humidity is low enough the layers can form within a span of three hours (Greene and Johnson, 1992b).

The timing of abscission, and the eventual initial dispersal distance of the seeds, are influenced by seasonality and the amount of foliage cover surrounding the parent trees. In closed forests, seeds must escape the canopy in order to disperse over long distances (Horn *et al.*, 2001; Nathan *et al.*, 2002). It is known that the wind conditions above the canopy play an important role in determining the dispersal distance of samaras (Horn *et al.*, 2001), although models struggle to predict the distance the seeds may travel, since they average over any strong but short-lived updrafts which may have a disproportionate effect on dispersal distance (Nathan *et al.*, 2002). The meteorological conditions above the canopy must also be considered in any models predicting long-distance dispersal of these seeds, as changes in foliage density impact wind dispersal by altering the wind flow patterns above the trees (Nathan and Katul, 2005).

In order to be uplifted above the canopy, seeds must be caught in consistent updrafts (Nathan and Katul, 2005); if they are not, the seeds will remain within the canopy and thus will not disperse over long distances (Horn *et al.*, 2001). Wind conditions above the canopy change

depending on the leaf-area index (LAI, measured as the one-sided leaf area per unit of ground area) (Nathan and Katul, 2005). Specifically, the mean windspeed above the canopy increases with increased LAI. However, more seeds are uplifted and reach higher elevations, thus potentially longer distances, when LAI is low. This discrepancy is due to the increasing windspeeds at higher altitudes (Nathan and Katul, 2005). These findings imply that seeds that abscise in early spring or late autumn, when LAI is lower, will disperse farther than seeds which abscise during the growing season (Nathan and Katul, 2005). However, Nathan and Katul (2005) also pointed out that, if seeds are not uplifted above the canopy to higher windspeeds or winds are not sufficiently strong during periods of lower LAI, seeds may disperse less far.

Despite samaras appearing to be optimised for wind dispersal, initial dispersal distances remain low, with the reported median dispersal distance for *Ulmus laevis* Pall. samaras at 21m, and 95% of samaras dispersing less than 30m (Venturas *et al.*, 2014). Although this distance may be enough for seedling establishment and the maintenance of local populations, it does not explain how wind-dispersed trees are capable of invading or colonising new environments. The 5% of seeds that dispersed farther than 30m are most likely to be responsible for geographic spread (Clark *et al.*, 1998). It has been theorised that the most far-reaching seeds disproportionately affect population dynamics. This theory has been supported by the Holocene spread of trees following the last ice age: the rarest and least observed, but longest, seed movements had a large effect on migration and allowed for the rapid expansion of habitat ranges post-glacially (Clark *et al.*, 1998). This theory is further corroborated by Nathan *et al.* (2002), who developed a new mechanistic model to predict long-distance dispersal of winged seeds during updrafts. Their model accurately predicted the vertical distribution of seeds from five tree species. They also performed simulations to predict the travel distance of the seeds (Nathan *et al.*, 2002).

261 Wind dispersal may account for a lot of the dispersive potential in winged seeds, especially
262 over long distances, but dispersal alone is not enough to allow species to spread. Establishment
263 must take place for successful colonisation to occur (Nathan *et al.*, 2002). If prevailing winds
264 are always oriented in the same direction, but the microclimates in which the seeds end up is
265 not optimal for germination, secondary dispersal may provide the mechanism for the seeds to
266 be brought to locations where they can establish. Secondary dispersal can also provide the
267 opportunity for seeds to disperse to locations where wind may not carry them. However, if we
268 do not increase the study into the secondary dispersal mechanisms of winged seeds, we will
269 never understand the potential spread and maintenance of populations of economically
270 important or highly invasive samara-bearing species.

271

272 *(2) Hydrochory as a mechanism for long-distance dispersal*

273 Dispersal by water is a very versatile process that does not require specialised adaptations
274 (Säumel and Kowarik, 2010). However, there has been only a small amount of research on how
275 samara morphology affects the seed's ability to disperse over water. This research has found
276 that across species, seeds with a low specific gravity and a high surface area float for longer
277 than other seeds (Säumel and Kowarik, 2013). This is as would be expected from physical
278 principles – with lower density reducing the force of gravity that must be opposed by surface
279 tension in order for seeds with higher density than water to float. The force of surface tension
280 of an object increases with its perimeter (something maximised for a given area by the long
281 thin shape of many samaras). Another study has shown that across three invasive, primarily
282 wind-dispersed species 95% of all seeds released during an experiment remained at the surface
283 for a three-hour period, at least (Säumel and Kowarik, 2010). A third study has found that, in

284 *Ailanthus altissima*, seeds which float for longer periods of time tend to be lower in mass
285 (Planchuelo *et al.*, 2016).

286 Although samaroid seeds are capable of remaining afloat for long periods of time (up to 20
287 days in lab conditions), and have been shown to be capable of travelling 4.05km on average in
288 natural conditions (Kaproth and McGraw, 2008), extended periods on or below the water's
289 surface appears to decrease the chances of successful germination (Kowarik and Säumel,
290 2008), although this is disputed (Kaproth and McGraw, 2008). The increased anaerobic
291 conditions most likely induce dormancy and reduce the viability of the seed. However, short
292 periods of flotation (up to 2 days) have been shown to increase the germination rate compared
293 to control seeds (Kowarik and Säumel, 2008). Therefore, hydrochory provides both benefits
294 and disadvantages for the long-distance dispersal and establishment of wind-dispersed seeds.
295 The relative importance of these will depend on how long the seed is in the waterbody, and
296 what fraction of that time involves floating rather than submergence.

297 Despite this handful of studies on the potential dispersive ability of winged seeds by water,
298 there are still many unanswered questions regarding hydrochory. If (as seems likely) samaras
299 positively affect buoyancy and thus samara-bound seeds are more capable of dispersing down
300 streams and rivers, or across larger bodies of water, then this may provide the opportunity for
301 long-distance dispersal when anemochory does not.

302 The volcanic island of Surtsey provided the informative study system for evaluations of
303 dispersive and colonisation potential of different plant (and animal) species. The island rose
304 from the sea between 1963 and 1967, following which the primary succession of all plant
305 species was recorded through extensive surveying of the island and its shores (Higgins *et al.*,
306 2003). A review of the data found that 78% of the plant species that arrived on the island were
307 brought by sea currents, despite only one quarter of those species being adapted for hydrochory

308 (Higgins *et al.*, 2003). Of the ten species (out of 48) that established on the island, half arrived
309 by, and were morphologically adapted for, dispersal by water (Higgins *et al.*, 2003). This
310 argues that species that are adapted for hydrochory are also adapted for the colonisation of
311 barren islands (Higgins *et al.*, 2003), but does not prove that only species that are adapted for
312 dispersal by water can colonise new regions successfully after such dispersal. The salinity, or
313 other properties of ocean water, may prevent species that are not adapted to survive such
314 conditions from germinating, but fewer specialist adaptations may be required to germinate
315 after dispersal over fresh water. However, it may be that the samara provides physical
316 protection to the seed from the adverse effects of saltwater. However, this potential mechanism
317 is dependent on how water-permeable the samara is – and how quickly it rots in water. The
318 natural process of decay of samara wings is entirely unstudied but understanding of this is vital
319 to improving our understanding of secondary dispersal of samara seeds.

320

321 *(3) Animal-mediated long-distance dispersal and seed predation*

322 Most studies equate seed removal by animal vectors to seed predation (Vander Wall, Kuhn and
323 Beck, 2005), despite zoochory being a well-known and important secondary dispersive vector
324 for many plant species (Vander Wall and Longland, 2004). It has also long been considered
325 that seeds that germinate have escaped all detection by animals, but little evidence has been
326 provided in support of this statement (Vander Wall, 1992). It is difficult to track seeds through
327 their secondary dispersal, and although not all seeds that are detected by animals will survive,
328 those that are cached have a larger chance of successfully germinating than those seeds that do
329 not experience secondary dispersal (Vander Wall, 1992).

330 Caching of seeds by animals, mainly small mammals, allows seeds to escape density-dependent
331 competition around the parent tree. A study on zoochoric secondary dispersal of pine samaras

found that rodents did not cache seeds within six metres of the source tree, and that most seeds were cached intact (Vander Wall, 1992). More than half (55.2%) of the caches found in that study produced seedlings, and the majority of the seedlings (82.6%) were healthy (Vander Wall, 1992). Seeds that were placed by the researcher on soil or needle litter were less likely to produce healthy seedlings (1% and 0.8% of seeds, respectively) (Vander Wall, 1992). Animal-mediated dispersal appears to be a critical component of seedling establishment in some samara-bearing species. However, the subject remains understudied in temperate angiosperms, and the few studies which have evaluated animal dispersal of primarily wind-dispersed seeds in tropical angiosperms have been mostly observational and comparative, rather than involving experimental manipulation to control for potential confounding factors.

A study on seed removal in Panama highlighted that seeds that are primarily wind-dispersed are less frequently removed by animals than seeds that are primarily animal-dispersed, and that most dispersal was done by invertebrates rather than vertebrates (Fornara and Dalling, 2005). This is a predictable result, as animal-dispersed seeds would be expected to attract more animal vectors than wind-dispersed seeds, and the wind-dispersed seeds used in this study had a lower seed moisture content than the other seeds; which may have influenced the decisions of the invertebrate seed predators (Fornara and Dalling, 2005). That does not mean, however, that the wind-dispersed seeds that are dispersed by animals are not significant to large-scale population dynamics (Clark *et al.*, 1998). If only one seed was dispersed to a new region by an animal vector where it could not have reached by wind dispersal alone, it would pave the way for the colonisation of an entirely new region.

Little is known about how the presence of the samara wing affects seed removal and predation. Although some studies have found that the presence of the wing does not affect removal by animals (Fornara and Dalling, 2005), others have found that seeds are removed or eaten more frequently if the seeds have already been separated from the samaras (Vander Wall, 1994).

357 Animals have also been known to discard the wing before removing the seed (Vander Wall,
358 1994; Tanaka, 1995), but not always (Vander Wall, 1992; Hulme and Borelli, 1999). Direct
359 comparisons between different species and thus seed morphologies, although common (Hulme
360 and Borelli, 1999; Fornara and Dalling, 2005; Jinks, Parratt and Morgan, 2012), are not useful
361 in determining the effect of seed morphology on removal rates. Seed predators may select seeds
362 for removal to maximise the energetic benefits, or they may prefer seeds based on chemical
363 composition (Jinks *et al.*, 2012); confounding any effect of samara-presence. Important though
364 these factors may be, these studies shed little light on how the samara structure affects seed
365 detection by animals as well as subsequent removal rates. We need experimental manipulation
366 to allow comparison of the fates of identical seeds with and without an intact samara.

367 Previous studies have found a positive relationship between seed mass and removal rates
368 (Vander Wall, 2003; Jinks *et al.*, 2012), and scatter-hoarding mammals have been found to eat
369 small seeds *in-situ* and store larger seeds in caches or larders (Vander Wall, 2003). Samara
370 seeds that have shed their wings, or whose wings are obscured by soil or plant litter may escape
371 animal detection (Vander Wall, 1994). It is likely that the presence of a samara structure has a
372 complexity of effects on likelihood of seed consumption by terrestrial granivores. The samara
373 will affect the microhabitat and orientation in which the seed sits on the ground. It will also
374 affect the detectability of the seed – the samara structure is likely to increase ease of visual
375 detection and possibly influence volatile emissions used in detection. Furthermore, the need to
376 excise the seed from the samara structure in order to consume the seed, and the greater
377 difficulty in transporting the seed with the samara still attached will reduce the attractiveness
378 of the seed as a food source. However, there have been observations of samaroid seeds of *Pinus*
379 *jeffreyi* Balf. and *Acer pseudoplatanus* L. being carried off with the wing still attached, mostly
380 by small rodents (Vander Wall, 1992; pers. obs.). The relative strengths of these mechanisms
381 will vary from system to system, but no study to date has sought to tease them apart for any

one system. Physical changes in the samara structure during decomposition will affect these mechanisms differentially too – so (again) improved understanding of samara decomposition would greatly aid understanding of the interaction of samara seeds and seed predators.

(4) Secondary anemochory

Samaroid seeds may be dispersed further by wind across the ground after the initial wind dispersal from the tree to the ground, if the conditions are right (Schurr *et al.*, 2005). However, pine and spruce samaras have been shown to be obstructed by a surface roughness of 2mm and less in wind tunnel experiments (Johnson and Fryer, 1992), and in a natural environment pine seeds were shown to be moved very small distances (of the order of centimetres) by the wind over a period of 37 days (Vander Wall and Joyner, 1998). Furthermore, the seed-mimics used by Vander Wall and Joyner (1998) were inedible and the wings were glued on, thus the wind dispersal distances they recorded may be inflated as more seeds would have been expected to be removed by animals under natural conditions. They also found that the majority of movement occurred within the first eight days, when samaras would move more than 5cm a day. However, after 8 days, most seeds were trapped in plant litter. In total, only 3% of seeds moved more than a metre (Vander Wall and Joyner, 1998).

When considering secondary anemochory, both natural and artificial wind sources must be taken into account. Von der Lippe *et al.* (2013) evaluated the movement of *Ailanthus altissima* seeds by the airflow of vehicles. They found that under wind-still conditions, seeds would move between 5.14m for one vehicle pass and 10.83m for eight vehicle passes, on average. Although this movement under un-natural wind conditions is clearly higher than that found under natural conditions (Vander Wall and Joyner, 1998), the seeds rarely moved off the road (von der Lippe *et al.*, 2013). Therefore, another dispersal mechanism would be required for the seeds to be

406 brought to a location suitable for establishment. Perhaps if the seeds were uplifted by the
407 vehicles' air stream and then carried further on natural wind gusts, they may disperse to such a
408 location, although this prediction has never been tested.

409 Secondary wind dispersal is also dependent on high-speed wind close to the ground, and the
410 maintained integrity of the wing structure (Schurr *et al.*, 2005). Overall, anemochory appears
411 a relatively ineffective secondary dispersal agent, especially for seeds whose dispersal
412 structures are easily damaged. However, again the empirical foundation for this conclusion is
413 slight. We would welcome studies like that of Vander Wall and Joyner (1998) that utilised a
414 greater variety of samaras, and surface conditions. It may also be that while samaras move little
415 under normal wind conditions – the samara confers enhanced dispersal potential under
416 unusually high wind conditions. Conversely, it may be that samaras actually retard secondary
417 dispersal by wind if they become waterlogged or trapped physically (on small plants for
418 example). Once again evaluation of this mechanism would be aided by understanding how the
419 samara changes physically after release from the parent plant.

420

421 *(5) Methods for tracking seeds*

422 Previous studies on long-distance dispersal in winged seeds have made use of a diversity of
423 methods. Perhaps the most prominent method used is inverse modelling; this statistical method
424 uses seed trap counts to model dispersal patterns (Bontemps *et al.*, 2013). However, this
425 method cannot be used for long-lived species like trees unless age is accounted for. This can
426 be done using synchronic sampling or estimating the dispersal of seeds from distinct cohorts.
427 Although this method is relatively easy to implement, seed traps can (and often do) miss
428 secondary dispersal events and thus these models frequently underestimate the total dispersal
429 ability (Bontemps *et al.*, 2013). Traps have to be placed prior to seed dispersal and thus their

430 placement (with respect to distance and most especially direction) can be suboptimal from a
431 sampling perspective. This will occur if this distribution of seeds ends up being quite different
432 from the distribution assumed in decision making about trap placement.

433 Many of the drawbacks of trapping methods can be overcome if seeds can be marked either by
434 paint or radiolabels to make re-finding them post-dispersal easier. Lemke, von der Lippe and
435 Kowarik (2009) tested multiple types of paint and application methods to determine which was
436 most appropriate for wind-dispersed seeds. They found that airbrushing techniques retained
437 colour the best over a one-month period, as well as minimising the weight gain of the seed.
438 Furthermore, they found that UV colours ensured that 85-90% of small seeds were found, and
439 100% of large seeds on both asphalt and grass (Lemke *et al.*, 2009). Radiolabelling with
440 Scandium-46 has also been proven successful in allowing the relocation of seeds (Vander Wall,
441 1992), with recapture rates between 40.6% and 83.0% across several years (Vander Wall,
442 2003). However, for many of the processes studied here the use of paint would need to be
443 carefully designed so as not to affect, for example, detection by seed predators, attractiveness
444 to seed predators, weight of the samara, and natural decay of the samara structure. As well as
445 the danger of modifying seed aerodynamics, this physical modification of seeds might well
446 influence the detectability and/or attractiveness of seeds to the seed predators and animal
447 secondary dispersers that are our focus. This methodology can also be very labour intensive,
448 and in the case of radioactive labelling require careful licencing and monitoring.

449 Lastly, parentage analysis can be used to characterise seed dispersal and germination patterns
450 (Godoy and Jordano, 2001). If seedlings are tested, the results are confounded by seed mortality
451 but do provide an accurate account of seedling establishment patterns (Bontemps *et al*., 2013).
452 A combination of seed tagging with either radioactive compounds (Vander Wall, 1992; Yi *et*
453 *al.*, 2014) or UV and fluorescent paints (Vander Wall and Joyner, 1998; Schurr *et al.*, 2005;
454 Reiter *et al.*, 2006) and parentage analysis (Godoy and Jordano, 2001; Bontemps *et al.*, 2013)

455 may be able to provide data on secondary dispersal and effective dispersal distances which
456 statistical modelling has not been able to provide.

457

458 *(6) Future research*

459 In this review, we have highlighted what is currently known about the primary and secondary
460 dispersal of winged seeds. The study of secondary dispersal in winged seeds has been often
461 neglected in favour of primary dispersal, although both processes help shape population
462 dynamics in many important plant species. An increase in research on secondary dispersal and
463 diplochory is critical if we are to understand the dispersive processes that influence the
464 population dynamics of samaroid species. First and foremost, any knowledge of the dispersal
465 potential of samaras will require an understanding of how the samara structure deteriorates.
466 This will be affected by the microclimate surrounding the seed, including weather conditions
467 such as wind speed, rainfall, and temperature. Once the wing deteriorates or detaches, the
468 dispersal potential of the seed will decrease (Vander Wall and Joyner, 1998), thus the majority
469 of dispersal most likely occurs while the wing is intact. However, there is no published research
470 on the length of time between abscission and deterioration in any samaroid species.

471 It is well-known that there is considerable variation of samara structure both between and
472 within species as well as within individuals (Peroni, 1994; Sipe and Linnerooth, 1995).
473 Although there has been some research on how this variation affects the primary dispersal of
474 samaras (Greene and Johnson, 1993; Sipe and Linnerooth, 1995; Delgado *et al.*, 2009), there
475 has been little research published on the impact of this variation on secondary dispersal, by any
476 vector (Planchuelo *et al.*, 2016). The intra-individual variation in samara shape and structure
477 may be an evolutionary response to different dispersal vectors, and if we determine the

478 relationship between the different structures and possible dispersal vectors it could reveal the
479 adaptive abilities of individuals.

480 There are also gaps in the knowledge in relation to every possible secondary dispersal vector
481 of samaras. Secondary wind dispersal has been previously studied and has established that most
482 winged seeds will be transported less than 30m under normal wind conditions over a period of
483 three years (Venturas *et al.*, 2014) or less than 1m over a period of a month (Vander Wall and
484 Joyner, 1998). However, seed movement along the ground has not been previously studied
485 under high wind conditions, which may provide a mechanism to transport samaras rapidly
486 across larger distances. For secondary dispersal on water, it has been well-established that
487 samaras are capable of flotation (Kowarik and Säumel, 2008; Säumel and Kowarik, 2010,
488 2013), but the potential travel distance has never been tested outside of lab conditions in any
489 species except *Ailanthus altissima* (Kaproth and McGraw, 2008; Säumel and Kowarik, 2013;
490 Cabra-Rivas, Alonso and Castro-Diez, 2014). The samaras of other species may show different
491 hydrodynamics. The effect of saltwater submersion on germination must also be established if
492 we are to determine whether samaroid seeds can disperse long-distances across seas or oceans
493 to colonise new lands.

494 The potential of seed predators to disperse samaras has been studied extensively in pines
495 (Vander Wall, 1992, 1994, 2003), and some comparative studies have been done in tropical
496 systems (Peña-Claros and De Boo, 2002; Fornara and Dalling, 2005). However, comparative
497 studies between species are not useful for determining the potential of seed predators as vectors
498 because of the inherent differences in chemical composition and thus predation rate between
499 different species of seed; instead, studies comparing the appeal of intact versus excised seeds
500 within species may be useful for determining the potential of seed predators as dispersal
501 vectors. Further studies like Vander Wall (1992), using radiolabelling to track samaras of
502 species outside the genus *Pinus*, could also assist in determining what percentage of seed

removal equals seed predation. The idea that seed removal always equals seed predation and thus seed death has been proven to be incorrect, although more research is required in a wider range of species to determine the importance of seed removal by predators to seedling establishment within these species.

Furthermore, although the phylogenetic dispersal of samaroid species has been determined (Manchester and O'Leary, 2010), the evolutionary reasons for the sparse distribution and the development of winged seeds remain unknown. Phylogenetic studies and genetic analysis could help us gain an understanding of the evolutionary mechanisms which have led to the development of winged seeds and may also be able to provide a reasoning for the use of different secondary dispersal vectors.

In conclusion, although we require more research on both the primary and secondary dispersal abilities of samaras, it is crucial that we give more attention to the second stage of dispersal, as well as the first. Ignoring these mechanisms due to a perceived inability to study them, either through complex modelling or methodologically complex experimentation or observation, will lead to misconceptions of the dispersal abilities of samaroid seeds.

Conclusions

1. Samaras, although believed to be primarily wind-dispersed, do rely on other dispersal vectors as well.
2. Seeds that are dispersed farther by wind on their initial dispersal may be lighter and thus be less successful at establishing in new environments.
3. Dispersal by water does not require specialist adaptations and can benefit germination.
4. Caching of seeds by granivores could increase the chances of successful germination.

5. The effect of the samara structure on diplochory and germination has not yet been well characterised, but we identify how significant strides can be made with relatively simple small-scale studies.
6. More research is required on the secondary dispersal vectors of winged seeds if we are to understand the life histories of samaroid species.

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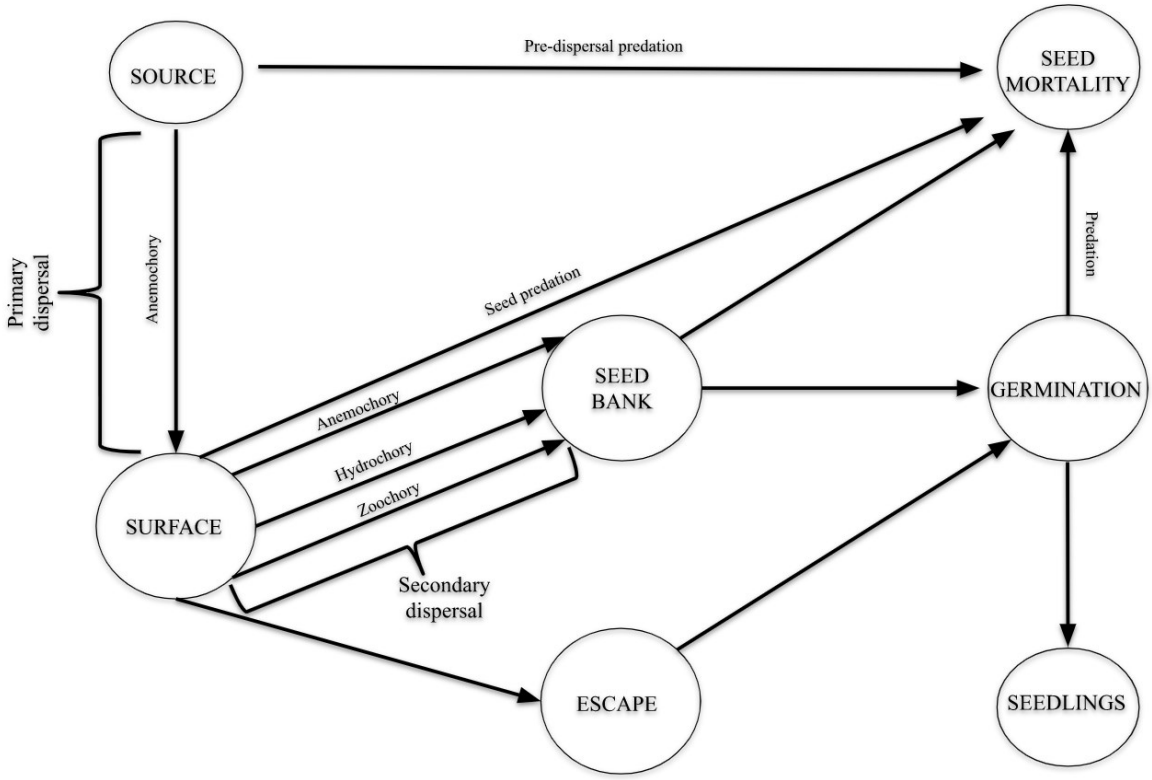
694 *Figure legends*



695

696 Figure 1: Possible pathways of winged seed fate. Although samaras will be initially dispersed
697 by anemochory, secondary dispersal may occur by any other dispersal vector. The most notable
698 (and studied) secondary dispersal vectors for winged seeds are anemochory, hydrochory, and
699 zoochory.

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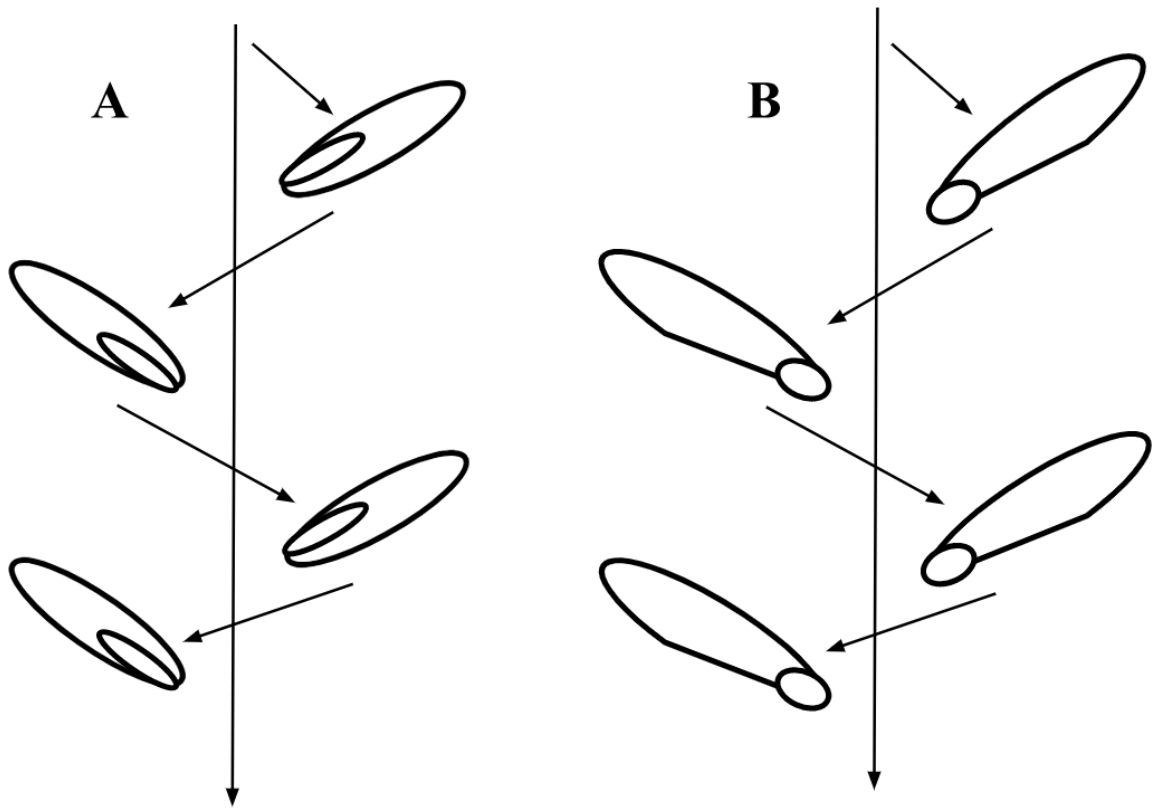

Figure 2: Movement of “rolling” versus “non-rolling” samaras. A represents a “rolling samara”, such as those of *Fraxinus* sp. The samara is symmetrical along the long axis and rotates along this axis while also spiralling downward along a vertical axis (Vogel, 2013). B represents a “non-rolling samara”, such as those of *Acer* sp. The samara is non-symmetrical and therefore only spirals downwards along a vertical axis (Vogel, 2013).