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Towards a clearer understanding of evolution of angiosperm dispersal: classical syndromes are subjective and should not be confused with mechanisms

A response to Jin *et al.* (2026): 'Evolutionary history and the global distribution of seed dispersal modes in angiosperms'

Jin *et al.* (2026) present and analyse a large compilation of 'seed dispersal modes' for global angiosperms and interpret the patterns as the macroevolution and global geography of biotic and abiotic dispersal mechanisms, with a strong emphasis on long-distance dispersal (LDD) (Jin *et al.*, 2026). However, the response variable used in their modelling is more heterogeneous than the mechanistic interpretations placed upon it allow. A single 'dispersal mode' is assigned to each species, with four options: zoochory, anemochory, hydrochory or autochory. Jin *et al.* rightly recognise the central importance of LDD in angiosperm evolution, and use their category 'autochory' to represent short-distance dispersal (SDD). Yet, their database is a heterogeneous compilation from various studies by different authors using different labels and criteria to place plant species into categories associated with seed dispersal (e.g. for European species, BioPop, LEDA, EuDiS and Lososová *et al.*, 2023 are all used as sources).

Heterogeneous source databases do not form a single coherent dispersal category

The different authors of these varied sources apply different thresholds, trait logic, and degrees of expert judgement. As a result, they often place a plant species into completely different dispersal categories. For example, EuDiS assigns 'dispersal syndromes' based on diaspore inspection, and the presence/absence of diagnostic traits (e.g. 'endozoochory syndrome' exclusively for a fleshy fruit, Vargas *et al.*, 2023). By contrast, BioPop uses different traits and gives more weight to empirical observations of dispersal to assign 'dispersal modes' (e.g. dry-fruited plants given an abiotic syndrome by other authors, but known to be dispersed by endozoochory, are labelled as 'endozoochory', Poschlod *et al.*, 2003).

A consequence of combining these sources without explicit harmonisation is that the resulting dataset contains inconsistencies that in our view affect interpretation. For example, they assign *Juncus bufonius* to endozoochory mode (from BioPop) and *J. hybridus* to autochory (from Lososová *et al.*, 2023), when these two taxa grow together, are morphologically indistinguishable, and can only be separated based on ploidy level (Williams-Marland *et al.*, 2026). Recently, for the flora of Surtsey, an island that emerged from the ocean in 1963, Wasowicz *et al.* (2025) demonstrated how EuDiS, Lososová *et al.* (2023) and a third classification system (Baseflor) assign different syndromes to the same plant taxa, and how all three systems fail to account for the LDD events required for colonisation. Hence, a global synthesis that merges such classifications into one dataset (Jin *et al.*, 2026) is not analysing a single coherent 'dispersal mode', but a mixture of subjective coding traditions.

Syndromes, mechanisms, and dispersal distances are different concepts

Two related but distinct issues arise. First, different source databases use different criteria and vocabularies. Second, by treating the different methods used in these sources as equivalent, Jin *et al.* risk treating dispersal syndromes as if they were directly equatable to realised dispersal mechanisms in nature. Indeed, 'dispersal mode' is an ambiguous term used in both contexts. Trait-based syndromes are effectively hypotheses about adaptations and likely dispersal pathways, not measurements of realised dispersal mechanisms. Vargas *et al.* (2023) rightly emphasise that their syndromes should *not* be equated with mechanisms, and that plants can disperse via different vectors to those implied by syndromes.

This distinction matters because Jin *et al.* interpret their results in mechanistic terms, as if their dataset directly identifies what vectors move seeds and by how far. By contrast, among documented dispersal interactions between animal and plant species in Europe, only 35% of plant species were assigned biotic syndromes in EuDiS, whereas at least 42% would be classed as autochory under Jin *et al.*'s methodology (Mendes *et al.*, 2024). It has been repeatedly shown that classical syndromes overlook persistent endozoochory for dry-fruited plants by herbivorous mammals and nonfrugivorous birds (Green *et al.*, 2022; Mendes *et al.*, 2026).

Polychory and rare long-distance events are lost when one mode is assigned per plant species

By removing polychory and choosing one 'dispersal mode' per species, Jin *et al.* further complicate interpretation of their results and make their 'biotic vs abiotic' analyses more uncertain. Many species disperse through both biotic and abiotic pathways, and the pathway that matters most for colonisation and range expansion is often not the most frequent mechanism but another that produces lower frequency, longer distance movements. Endozoochory, for example, often provides maximum dispersal distances for dry-

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fruited plants (Green *et al.*, 2022). This problem is not new: Ozinga *et al.* (2004) showed that dispersal potential in plant communities depends on environmental conditions and that species cannot easily be reduced to a single LDD pathway. Collapsing multi-pathway dispersal to a single 'most common' category therefore removes information about exactly the kinds of events that generate LDD and colonisation and are often the most evolutionarily significant.

Autochory and zoochory are especially problematic composite categories

Autochory is central to Jin *et al.*'s framework because it is treated as the SDD counterpart to their constructed 'LDD proxy'. In principle, autochory means true self-dispersal (the plant provides the energy, e.g. by ballistic release). However, in practice, the autochory bin in their database contains a large block of records that are not associated with any dispersal mechanism, but instead an explicit statement of uncertainty. Their dataset includes 5197 species labelled as 'autochory' based on Lososová *et al.* (2023), even though their original description is 'local non-specific dispersal'. These represent 56.3% of autochory records in Jin *et al.*'s database.

This matters because Jin *et al.* then contrast 'autochory' against their LDD proxy as if it were a clean mechanistic divide. Our Surtsey study illustrates the problem. Surtsey is an oceanic island >30 km offshore, so colonisation events necessarily involve LDD. Yet in our analysis, the same source (Lososová *et al.*, 2023) placed 67% of Surtseyan colonisers into 'local non-specific dispersal'. This example is not presented as globally representative, but as an empirical warning that 'unknown', 'local' or 'nonspecific' categories can contain species capable of LDD. When 'short-distance' contains a large 'unknown/nonspecific' block, macro-evolutionary claims about frequent transitions out of autochory, or geographic gradients in 'LDD', may be artefacts of category design and source tradition, rather than reflecting genuine dispersal mechanisms.

A similar problem applies to 'zoochory mode', in which Jin *et al.* pool very different processes, including endozoochory, epizoochory, caching, and myrmecochory, which provide different dispersal distances. Ant dispersal is widely considered to be SDD (Vargas *et al.*, 2023), whereas vertebrates can move seeds much farther. Yet Jin *et al.* treat myrmecochory as part of their LDD group that they contrast with autochory as SDD. Myrmecochory occurs 1156 times in their dataset (7.9% of zoochory records), so their 'zoochory' bin contains a sizeable short-distance component. Hence, treating zoochory as a uniform proxy for LDD risks combining processes that differ greatly in dispersal distance. We therefore do not argue that zoochory is uninformative. Rather, we argue that zoochory is too broad to serve as a uniform LDD category unless its component mechanisms are analysed separately (e.g. Mendes *et al.*, 2026) or weighted by expected dispersal distance. Hence, we suggest that 'zoochory = LDD' is not a valid assumption, and that neither the 'biotic vs abiotic' transitions nor the 'SDD vs LDD' transitions of Jin *et al.* are likely to be robust.

Recent synthesis work further shows that current knowledge regarding zoochory is strongly compartmentalised among disperser guilds, mechanisms, and plant types, reinforcing the need to separate endozoochory, epizoochory, synzoochory and myrmecochory rather than pooling them into one 'zoochory' category (Mendes *et al.*, 2026).

Classical syndrome coding underestimates dry-fruited endozoochory

A further difficulty is that the datasets combined by Jin *et al.* mix classical syndrome classifications based on diaspore morphology with more mechanistic classifications based on empirical observations of seed dispersal. Classical syndrome coding typically treats endozoochory primarily as a fleshy-fruit phenomenon, whereas some source datasets (e.g. BioPop) do include dry-fruited species where empirical evidence for endozoochory is taken into account. This mixture is itself important: the resulting 'zoochory' category combines records inferred from morphology with records supported by observed mechanisms.

Evidence for internal transport of dry-fruited diaspores by birds and mammals is long-standing and substantial (Proctor, 1968; Green & Wilkinson, 2024; Mendes *et al.*, 2026), and modern work continues to show that herbivorous mammals and waterbirds in particular disperse many plants internally and sometimes over extreme distances that exceed expectations based on their abiotic syndromes by several orders of magnitude (Albert *et al.*, 2015; Viana *et al.*, 2016; Lovas-Kiss *et al.*, 2023). Since a major part of the zoochory (including LDD) realised in nature is systematically under-recognised by reliance on classical syndromes, the syndrome-coded 'biotic dispersal' construct in Jin *et al.*'s analyses may not reliably represent animal dispersal mechanisms at global scale, especially outside the tropics.

The results presented by Jin *et al.* largely echo previous work showing how fleshy fruits are more dominant among angiosperms in the tropics and in moist climates (Chen *et al.*, 2017), but these trends should not be interpreted as evidence for zoochory as a whole without further qualification. Jin *et al.* suggest that 'suitable dispersal agents [for zoochory] are scarce' outside tropical regions, when in fact the opposite may be true for some vectors. For example, migratory waterbirds provide extreme LDD and are most abundant at high latitudes (Gaston & Blackburn, 1996; Viana *et al.*, 2016). Avian endozoochory of dry fruits explains most plant colonisation of Surtsey in the sub-Arctic (Wasowicz *et al.*, 2025). Increased transitions to fleshy fruits in response to paleoclimate do not necessarily imply strengthened biotic interactions, since endozoochory of dry and small seeds is widespread (although often understudied) and precedes the evolution of fleshy fruits (Salgado *et al.*, 2017). Seed plants evolved >350 million years ago (Ma) when tetrapods had already colonised land. Herbivorous reptiles evolved *c.* 300 Ma, providing good LDD vectors (Yoshikawa *et al.*, 2019). It thus seems unlikely that seed plants would only evolve adaptations for zoochory with the arrival of fleshy fruits >200 Myr later.

Towards more robust global dispersal databases

The issues raised here do not imply that global dispersal syntheses are unattainable. Rather, they show that future analyses would

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benefit from distinguishing several layers of information that are currently often collapsed into a single species-level label. These layers include: diaspore traits, such as fruit type, seed size, appendages, buoyancy, adhesion structures, and elaiosomes; inferred syndromes, meaning trait-based hypotheses about likely vectors; observed mechanisms, meaning empirical records of dispersal by animals, wind, water, ballistic release, or other vectors; and dispersal-distance evidence, especially measured or modelled distances relevant to colonisation and range expansion, assigned to specific mechanisms whenever possible. Where possible, trait data should be quantified according to standardised protocols (e.g. measuring terminal wind velocity, buoyancy, or resistance to simulated gut passage, van Leeuwen *et al.*, 2023), or at least cross-calibrated between different observers. Morphological diaspore traits should also be documented with standardised image databanks. Raw data on seed dispersal distances should be placed in the public domain, so their distributions can be fully explored to avoid reliance on simple measures of maxima (sensitive to sample size) and arithmetic means (inappropriate since distances are not normally distributed).

These layers should not be collapsed into a single species-level label without retaining uncertainty. A practical global database could therefore record multiple dispersal pathways per species, preserve source identity, and flag whether each record is trait-inferred or empirically observed. Such a structure would allow macroevolutionary analyses to ask clearer questions: not only which syndrome is most common but also which traits, vectors, and rare dispersal pathways are associated with colonisation and range expansion.

In summary, we question the reliability of conclusions made by Jin *et al.* They describe the macroevolution and global geography of imprecise 'mode' labels rather than the macroevolution and geography of dispersal mechanisms, consistent traits, or realised LDD. Since their response variable is constructed from subjective and heterogeneous sources with different criteria, simplified by removing polychory, and used to define 'LDD' by category membership, their conclusions about dispersal mechanisms or dispersal distances cannot yet be considered robust. The Surtsey case provides a clear empirical warning: even in a tractable colonisation system, syndrome-coded dispersal categories do not explain colonisation success, and therefore cannot be assumed to provide mechanistic information at broader spatial or temporal scales (Wasowicz *et al.*, 2025). Given the current lack of empirical data on dispersal mechanisms for each angiosperm species from many parts of the world, we suggest that the most practical and reliable way forward is not simply to expand existing syndrome tables but to build databases that distinguish diaspore traits, observed vectors, uncertainty, and dispersal-distance evidence. Such a framework would differ considerably from the approach used for the database analysed by Jin *et al.* and would make future global analyses of angiosperm dispersal more interpretable and more useful.

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Competing interests

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