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Evolution of dispersal strategies in conifers: Functional divergence and convergence in the morphology of diaspores

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ABSTRACT

We provide an integrative view of the evolution of dispersal strategies in modern conifers, by characterizing and examining the phylogenetic distribution of diaspore functional morphotypes, diaspore structural compositions, seed coat modifications, and dispersal syndromes using the phylogeny of Leslie et al. (2012). We first classified diaspores into nine functional morphotypes, which represent overall dispersal strategies that encompass the multiple phases of dispersal. We mapped these morphotypes, the eight different structural compositions of diaspores, two types of seed coat modifications, and the four recognized dispersal vectors onto the phylogeny and used maximum parsimony and maximum likelihood to infer ancestral states and assess shifts in dispersal characteristics. We found that structural traits (diaspore composition and seed coat modifications) are more conserved than ecological traits (functional morphotype and dispersal vector/syndrome). Almost all diaspore functional morphotypes have multiple independent origins, with several instances of parallelism (using the same structures to generate a morphotype) within families, but generally functional convergence (using different structures to generate a morphotype) between families. Within extant conifer families, shifts in the dispersal syndrome occur most frequently with simultaneous shifts in both diaspore morphotype and composition. Shifts from winged wind-dispersed to fleshy animal-dispersed diaspores are infrequent and occur only in the direction from wind to animal dispersal. Shifts to gravity or water dispersal occur from both wind and animal dispersed diaspores, concurrent with the loss of dispersal structures from the diaspore. Within both wind and animal-dispersed syndromes, shifts between functional morphotypes represent further differentiation of overall dispersal strategies, and occur most frequently without corresponding changes in the structural composition of the diaspore. The recurrent evolution of distinct functional morphologies suggests that there are local adaptive maxima that balance tradeoffs in traits related to both transport and establishment, within developmental limitations. Overall, our results suggest that the ancestral diaspore type for all modern conifers consisted only of a seed. Conifers diversified in their dispersal strategies through seed coat modifications or by the incorporation of various parts of the seed cone into the diaspore, with the modern conifer families independently evolving their characteristic diaspore compositions. Almost all functional morphotypes were present prior to the Cenozoic in at least one lineage, with more recent shifts in morphotypes representing functional convergence or parallel evolution rather than ecological novelties.

1. Introduction

Dispersal is an important process that shapes ecological and evolutionary patterns, and accordingly it has been the focus of a large body of theoretical and empirical literature. The ability of plants to effectively disperse their progeny across a temporally or spatially heterogeneous landscape has profound effects on the geographic distribution of taxa (Ackwood et al., 1993; Dynesius and Jansson, 2000; Edwards and Westoby, 1996; Longton, 1992; Rumeu et al., 2014), influences range shifts in response to climate change (Clark et al., 1998; Davis and Shaw, 2001; Higgins and Richardson, 1999; Thuiller et al., 2008), controls gene flow and the genetic structure of populations (Bacles et al., 2006; Hamrick et al., 1993), and

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ultimately influences the potential for both speciation and extinction (Leimar and Norberg, 1997; Van Valen, 1971). Dispersal is a multi-phase process (pre-departure, departure, transience, and settlement; see Lehouck et al., 2012), and seed plants exhibit a wide array of adaptations that facilitate all phases of the dispersal of their seeds. The collection of adaptations resulting in the overall phenotype of the diaspore (the seed plus any additional dispersing structures) thus represents a multivariate dispersal "strategy," which presumably confers an evolutionary benefit and reflects tradeoffs between adaptations related to the various phases of dispersal (e.g., Alcántara and Rey, 2003; Levin et al., 1984; Manzaneda et al., 2009; Schupp, 1995). Different dispersal strategies are shaped by, and in turn shape, the ecological interactions and structure of communities (Levine and Murrell, 2003; McPeek and Holt, 1992; Nathan and Muller-Landau, 2000; Starrfelt and Kokko, 2012).

The transport phase of dispersal (departure plus transience) is an important driver of plant distributions, in that it controls the total possible spatial distribution of a subsequent generation. It is perhaps for this reason that studies of diaspore phenotypes have focused primarily on their relation to mechanisms of movement. The most widely used dispersal classification, dispersal syndromes, is based upon suites of diaspore characters that relate to the plant's primary dispersal vector: by wind, water, biota, or the plant itself (including simply gravity) (Howe and Smallwood, 1982; Van der Pijl, 1982). Respectively, these syndromes are referred to as anemochory, hydrochory, zoochory, and autochory (barochory). These broad categorizations are useful for understanding alternate selection regimes and coarse differences in local patterns of dispersal. Within a given syndrome, different morphologies, such as various wing morphologies (Green, 1980) and fruit shapes and sizes (Geldenhuys, 1992; Ridley, 1930), convey further differences in seed dispersal patterns that relate to various ecological strategies. Given that movement of the seed from the parent plant to a potential germination site is only one component of the multiphase process of dispersal, dispersal syndromes alone fall short of explaining the multi-functionality and ecological importance of diaspores. In particular they fail to recognize that diaspores reflect adaptive tradeoffs related to the relative importance of different phases in the overall dispersal strategies of taxa.

The relationship between diaspore morphology and dispersal strategies, including the distribution of dispersal syndromes between and within families, has been studied primarily in extant and fossil angiosperms (e.g., Bremer and Eriksson, 1992; Eriksson et al., 2000; Manchester and O'Leary, 2010; Ridley, 1930; Tiffney, 1986a,b; Tiffney and Mazer, 1995; Van der Pijl, 1982; Xiang et al., 2014). In comparison, conifers have received relatively little attention (but see Benkman, 1995; Givnish, 1980; Herrera, 1989; Leslie et al., 2013a; Tiffney, 1986a; Tomback and Linhart, 1990), even though they also exhibit a variety of strategies for seed dispersal. Conifers comprise a major clade of seed plants that has existed for over 300 million years (Taylor et al., 2009), and this longevity provides an ideal model system for studying the evolution of dispersal. They have a large, yet computationally manageable number of extant taxa; their modern relationships are fairly well known (e.g., Leslie et al., 2012); and they occupy a wide range of habitats in tropical to boreal environments (Eckenwalder, 2009). Furthermore, there is a large theoretical and empirical foundation for the homology of coniferous reproductive structures (e.g., Escapa et al., 2008, 2013; Florin, 1951; Rothwell et al., 2011; Serbet et al., 2010). The latter is particularly important because adaptations for different dispersal methods are achieved through seed coat modifications or by incorporating various parts of the seed cone into the dispersal unit. Thus, analyzing dispersal structures within a phylogenetic framework can provide a novel consideration of adaptations that have shaped dispersal ecology in conifers, past and present.

The distribution of broad dispersal syndromes across living conifer taxa has been studied in relation to breeding systems (Donoghue, 1989; Givnish, 1980; Leslie et al., 2013a), biogeographic distributions (e.g., Rumeu et al., 2014), and taxonomic diversity (Herrera, 1989; Leslie et al., 2013a). Notably, however, the morphology of conifer diaspores remains largely unstudied from an evolutionary perspective across the conifer tree of life (but see Leslie, 2011, for discussion of cone functional evolution). It is clear, for instance, that fleshy diaspores are not all constructed from the same structures or developmental processes (e.g., Englund et al., 2011; Florin, 1951, 1954; Tomlinson and Takaso, 2002), yet diaspores in separate families can have strikingly similar phenotypes. In these cases, the observed similarities may not be due to common ancestry. Such homoplasy has important implications from an evolutionary-ecological perspective, as distantly related taxa with similar diaspores point towards the repeated evolution and refinement of phenotypes that represent particularly effective dispersal strategies. Similar phenotypes can develop independently in different lineages by either modifying the same structures following the same developmental pathway (parallelism), or by modifying completely different structures to achieve a similar overall form (functional convergence). While both may indicate that taxa face similar ecological pressures (Losos, 2011), parallelisms may also result from genetic and developmental constraints on variation (Pearce, 2011; Wake et al., 2011), functional tradeoffs in development (Greene and Johnson, 1993), and optimization of energetic costs to the parent plant (Chapin et al., 1993).

The goal of our study was to conduct a comprehensive analysis of diaspores as they relate to different dispersal strategies across living conifers within a phylogenetic context. The four major aspects explored here are (1) *diaspore composition* – which tissues or structures are included in the dispersal unit, (2) *seed coat modifications* – whether the seed coat has prominent dispersal adaptations (3) *diaspore functional morphology* – the overall phenotype as it relates to functional aspects of the multiple phases of dispersal, and (4) *dispersal syndrome* – the primary vector responsible for the transport phase of dispersal. By studying both the underlying structural (1–2) and emergent ecological (3–4) characteristics of diaspores, we investigated four main questions: (1) What is the diversity and distribution of diaspore functional strategies, as inferred by functional morphology, in extant conifers? (2) To what extent are similar diaspore functional morphologies in extant conifers likely due to convergence or parallelism? (3) Are dispersal traits fairly conserved within lineages, and if so, what are the inferred ancestral states for dispersal syndromes, diaspore functional morphology, composition, and seed coat modifications? (4) What is the frequency and pattern of evolutionary transitions between diaspore functional morphologies and dispersal syndromes?

To answer these questions, we provide a classification of conifer diaspores based on functional morphology and structure in the broader context of primary seed dispersal syndromes. Using this classification, we explore the phylogenetic distribution of diaspore functional morphotypes, diaspore composition, seed coat modifications, and dispersal syndromes by mapping characters onto a phylogeny of extant conifer taxa. We use one of the most complete conifer phylogenies to date, produced by Leslie et al. (2012), based on nuclear and chloroplast genes and with fossil calibration of divergence times. This phylogeny includes all extant genera (and ~80% of species), thus comprising a comprehensive framework within which trait evolution can be traced across extant lineages. Our findings are compared to known fossil conifer diaspores, and the evolutionary and ecological implications are discussed. Considering the influence of dispersal on local, community, regional, and biome-level processes, we anticipate that understanding the phylogenetic distribution of diaspore functional morphologies, coupled with more in-depth studies of their dispersal potential or real-