The Evolution of Cone and Seed Size in Serotinous Conifers

Karishma Swarup[1], Andrew B. Leslie[2]

[1]Department of Earth, Environmental, and Planetary Sciences, Brown University, Providence, RI 02912. [2]Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912.

Background

Plants have evolved a wide variety of ways to move their seeds, from delicate parachute-like structures to large edible fruits. **Serotiny**, or the **retention of seeds in unopened fruits or cones**, is a specialized dispersal mechanism found in a number of groups where seeds are kept on the parent plant and released *en masse* following a disturbance event like a wildfire. Serotiny can be a successful ecological strategy, but it is thought to require a correlated suite of additional traits such as robust woody structures to protect the long-held seeds. These correlations may constrain the evolution of serotiny or favor its appearance in certain lineages, but they have rarely been tested in a phylogenetic framework.

Research Questions

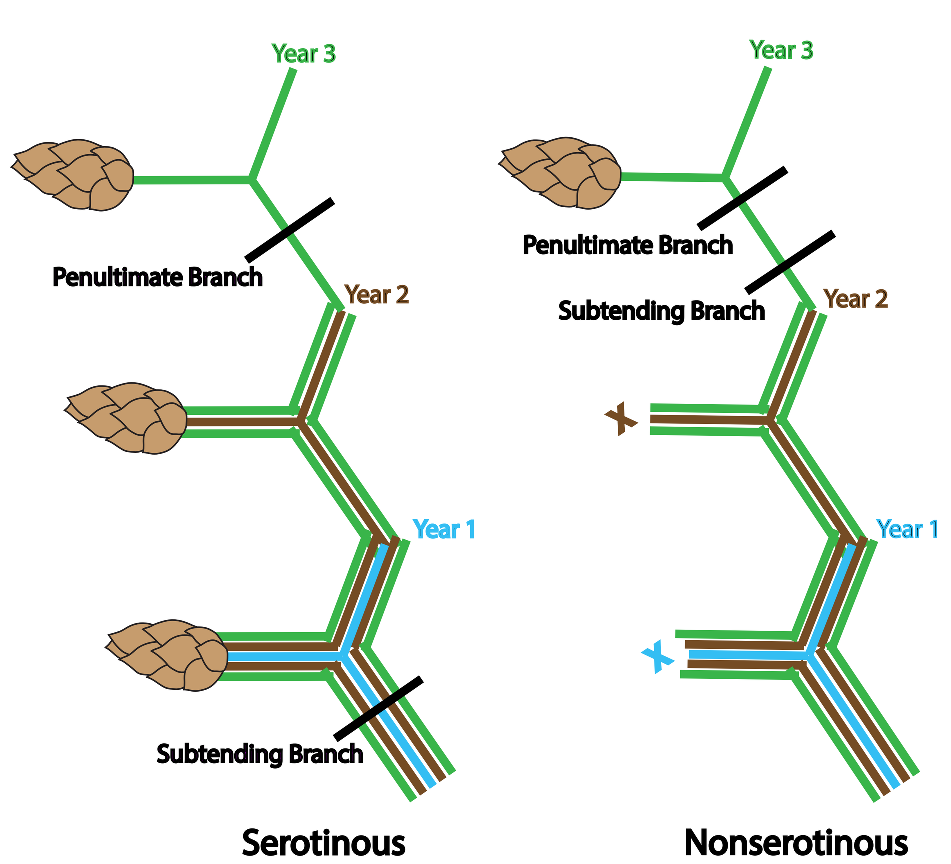
1) Do serotinous species have more robust seed protecting structures than nonserotinous relatives?

2) Do serotinous species differ in other important reproductive traits, specifically seed size?

We use conifers of the Cupressaceae (cedar) clade as a study system to address these questions. The group has their seeds contained in woody cones of different sizes (see right)

Methods

We measured cone size and seed size from 73 species (~ 5 individuals from each species) housed in the Harvard University Herbaria collections, recording length and width of seed cones and the seeds they contained. We then estimated seed and cone volume using these measurements as major and minor axes of an ellipsoid.



How did we assess serotiny?

Cupressaceae cones occur at the tips of shoots, so retained cones are subtended by larger diameter branches. To determine whether cones were retained, we measured the ratio between the diameter of the **subtending branch** of a cone, and the diameter of the **penultimate branch** of vegetative shoots; in retained species, this *cone-branch ratio* was larger. Whether species were fully serotinous (retained + closed cones) was based on direct and published observations

Data

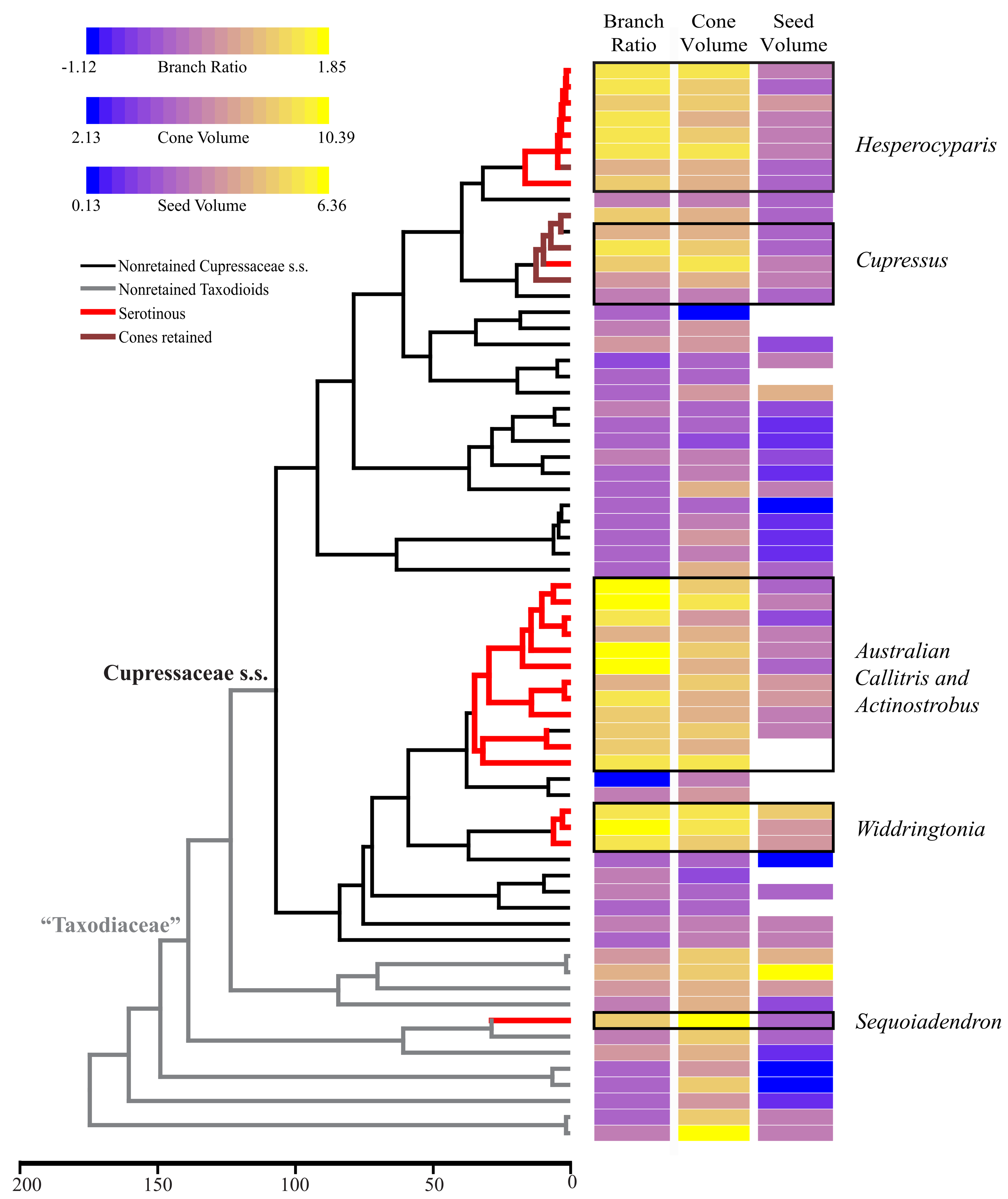


Figure 1. Time-calibrated Cupressaceae phylogeny (based on Leslie et al., 2012) showing the distribution of cone retention, full serotiny (cones both retained on the tree and closed), cone-branch ratio, log cone volume, and log seed volume. Serotinous genera are specifically indicated and their species are outlined with a black box.

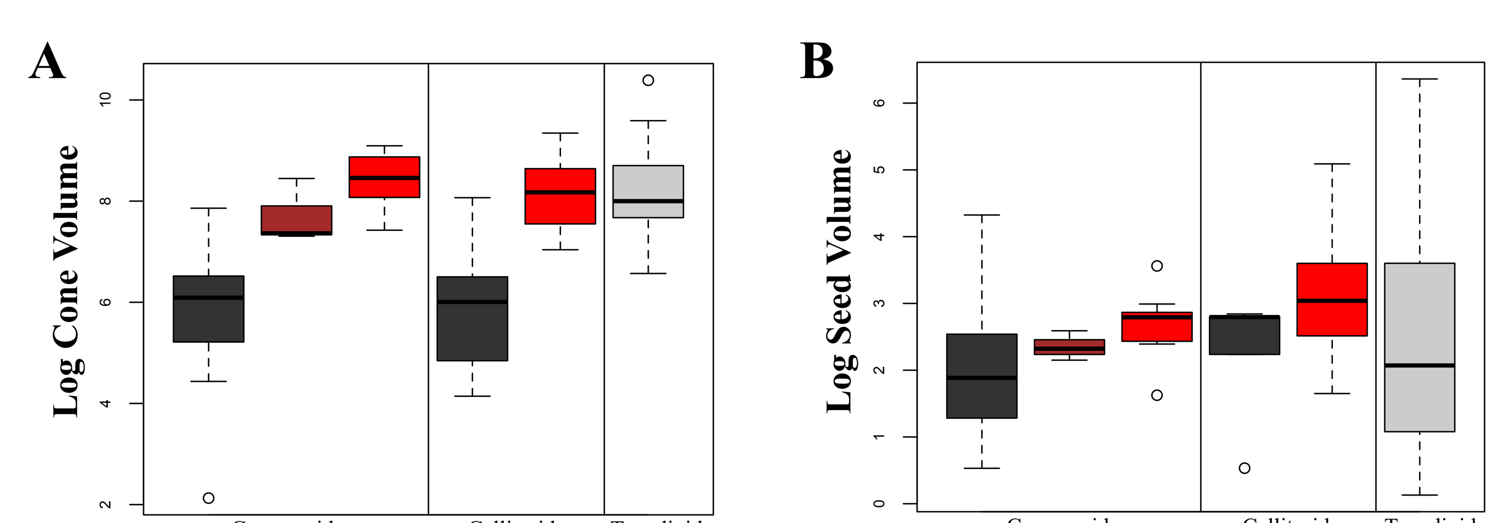


Figure 2. Box plots showing cone volumes (**A**) and seed volumes (**B**) in species with nonretained cones (black in Cupressaceae s.s. and gray in "Taxodiaceae"), retained cones (brown), and full serotiny (red; cones both retained on the tree and closed). Species are broken down by major group or clade.

Results

Serotiny evolved once in early-diverging Cupressaceae lineages ("Taxodiaceae") and four times in derived lineages (Cupressaceae *sensu stricto*). Cone retention without full serotiny evolved once (in the genus *Cupressus*).

Within Cupressaceae *s.s.*, species with retained cones consistently have larger cones, and fully serotinous species have the largest cones. The same pattern is found in "Taxodiaceae", but cones are generally larger and there is only a single serotinous species.

Serotinous species tend to have larger seeds, but this is due to a general relationship between seed and cone size.

Cone retention and serotiny is not a significant predictor of seed size ($p = 0.64$) in a multiple phylogenetic regression including cone volume.

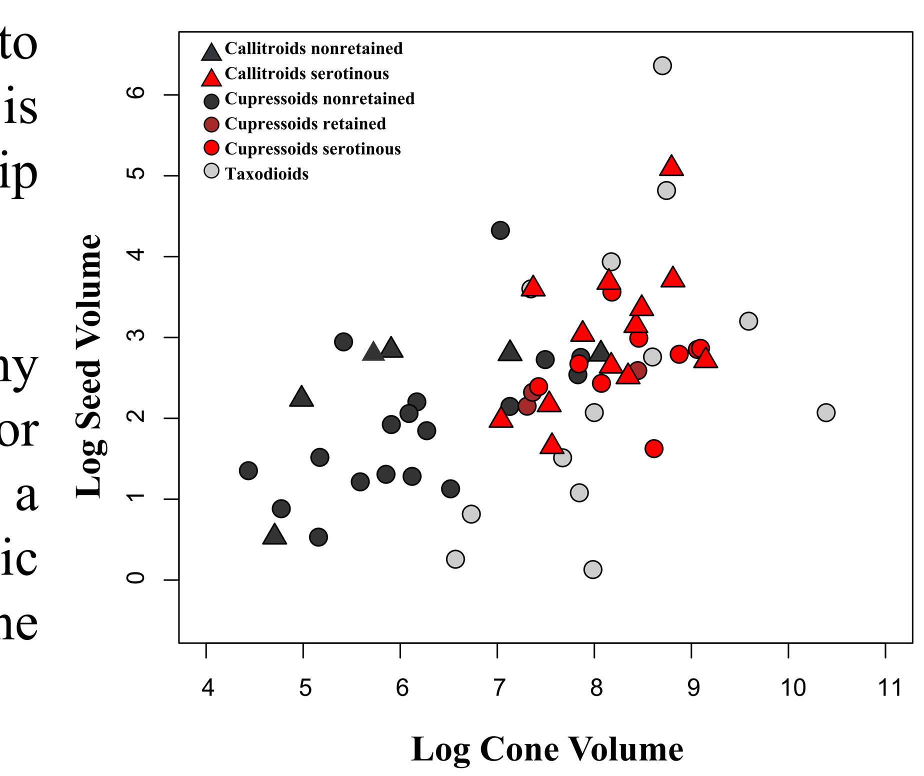


Figure 3. Bivariate plot showing relationship between Cupressaceae cone volume and seed volume among species. Seeds in Cupressaceae *s.s.* show a positive scaling relationship with cone volume, but serotiny or cone retention does not significantly alter this relationship.

Discussion

Within Cupressaceae, serotinous species and those that retain their reproductive structures on the plant repeatedly evolved larger cones. This is consistent with results of other studies suggesting that more robust cones protect seeds from disturbance events associated with serotiny, such as frequent wildfires (Ladd et al., 2013). These changes appear to have little direct effect on the evolution of seed size itself. Adaptations to a serotinous dispersal strategy then appear to primarily change how seeds are packaged rather than other fundamental aspects of plant dispersal biology.

Acknowledgements and Citations

We would like to thank the Harvard University Herbaria and the Brown Undergraduate Research and Teaching Award program.

Ladd, P. G., J. J. Midgley, and A. P. Nield. 2013. Serotiny in southern hemisphere conifers. *Australian Journal of Botany* 61: 486-496.

Leslie, A. B., et al. 2012. Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings of the National Academy of Sciences* 109: 16217-16221.