

Do latex and resin canals spur plant diversification? Re-examining a classic example of escape and radiate coevolution

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Handling Editor: Richard Shefferson

Abstract

1. The association between increased lineage diversification rates and the evolution of latex and resin canals is widely cited as a paradigmatic example of Ehrlich and Raven's 'escape-and-radiate' hypothesis of co-evolution. However, it has been over a quarter-century since the original study, and updates to phylogenetic comparative methods, plant molecular systematics, and phenotypic data warrant a reassessment of this classic finding.
2. We gathered data on latex and resin canals across 345 families and 986 genera of vascular plants and conducted a multi-scale test of the association between these traits and lineage diversification rates. At a broad scale (across clades), we used sister-clade comparisons to test whether 28 canal-bearing clades had higher net diversification rates than their canal-lacking sister clades. At a finer scale (within clades), we used ancestral state reconstructions and phylogenetic models of lineage diversification rates to examine the relationship between trait evolution and the timing of diversification rate shifts in two better-characterized clades – Araceae and Papaveraceae.
3. At both scales of our analyses we found poor support for the predicted relationship between diversification and the evolution of latex and resin canals. Follow-up analyses clarified that the qualitative change between our results and those of the Farrell et al.'s classic study is not the result of different phylogenetic comparative methods. Instead, the differences are attributable to updates to plant systematic hypotheses and new data on laticifers and resin canal presence/absence.
4. *Synthesis.* Our updated study reveals that there is no longer strong evidence for latex or resin canals as general, consistently replicable drivers of species diversity across plants. However, we cannot rule out a relationship in all groups. We therefore argue that theoretical and empirical work aimed at understanding ecological factors that condition 'escape-and-radiate' dynamics will allow for more nuanced tests of the hypothesis in the future.

KEYWORDS

coevolution, diversification, escape and radiate, evolution of anti-herbivore defenses, key innovation, latex, phylogenetics, plant-herbivore interactions

1 | INTRODUCTION

In their landmark paper, Ehrlich and Raven (1964) changed the field of evolutionary ecology by proposing a novel hypothesis of co-evolution. Now termed 'escape-and-radiate' coevolution (Thompson, 1989), the hypothesis aims to explain plant diversity by invoking a co-evolutionary tango between herbivores and plant defenses. Specifically, they posited that the innovation of novel defenses allows plants to 'escape' constraints of herbivory and 'radiate' (or persist under reduced extinction rates) in newly opened niche space. Ehrlich and Raven's ideas remain prominent in current eco-evolutionary thinking, and many studies have tested various associations between plant defensive traits and increased lineage diversification (diversification = speciation – extinction) (reviewed in Janz, 2011; Suchan & Alvarez, 2015). Despite an extensive literature on the topic, evidence for 'escape-and-radiate' dynamics remains mixed, and there remains a paucity of data testing these ideas for the majority of defensive traits (Futuyma & Agrawal, 2009; Suchan & Alvarez, 2015). Here, we revisit one of the most iconic examples of escape-and-radiate dynamics: the association between lineage diversification and the evolution of latex and resin canals, which store and release sticky exudates that defend plants against herbivores (Farrell, Dussourd, & Mitter, 1991).

Both latex and resin are potent plant defenses that represent model traits for studying the evolution and ecology of plant-herbivore interactions (Agrawal & Konno, 2009). Although they differ in their anatomy (latex is stored in elongated cells called laticifers, whereas resin is stored within intercellular spaces called canals or ducts) and chemistry (latex is rich in proteins, alkaloids and sugars, whereas resin is rich in terpenoids or phenolics), both latex and resin are stored in pressurized cellular structures that play active roles in defense (Agrawal & Konno, 2009; Konno, 2011; Prado & Demarco, 2018; Ramos, Demarco, Costa Souza, & Freitas, 2019). Notably, pressurization allows latex and resin to be released when chewing herbivores damage the leaves, acting as an inducible defense via toxicity and by physically gumming-up herbivore mouthparts. Thus, despite anatomical and chemical differences, the functional similarity of laticifers and resin canals in pressurizing and exuding latex and resin, respectively, has led several authors to argue that these traits should be considered as a single defensive syndrome (Dussourd & Denno, 1991; Farrell et al., 1991). There is a rich body of work linking these traits to reduced herbivory across plants (reviewed in Konno, 2011; Phillips & Croteau, 1999), and documenting the evolution of behaviour or physical 'counter-defenses' in herbivores (adaptations that allow herbivores to circumvent the latex and resin defenses, such as trenching and notching behaviours that depressurize canals before feeding (Dussourd & Denno, 1991). Together, this body of work suggests a strong role for latex and resin canals as key innovations in the escape-and-radiate process.

Latex and resin canals are also ideal candidates for conducting tests of the 'escape-and-radiate' hypothesis because each shows

high levels of evolutionary convergence across plant lineages (Agrawal & Konno, 2009; Langenheim, 2003). Latex and resin canals have originated at least 40 independent times (Farrell et al., 1991), and latex occurs in about 10% of flowering plant species (Agrawal & Konno, 2009) while resin occurs in roughly 53% of plant orders (Langenheim, 2003). Farrell et al. (1991) took advantage of the highly convergent histories of laticifers and resin canals across vascular plants to test for patterns consistent with trait-associated shifts in lineage diversification rates. Farrell et al. (1991) compared 16 pairs of sister-clades that differed in the presence or absence of laticifers/canals, performing a sign test to evaluate whether there was evidence for enhanced species richness in clades with laticifers/ducts relative to sister clades without laticifers/ducts. By controlling for clade age using sisters, their design allowed for the comparison of net diversification rates across many independent evolutionary events, offering an intuitive and replicated test of the escape-and-radiate hypothesis. Their results were striking: 13 of the 16 comparisons revealed higher species richness when canals were present, supporting the prediction that the origins of plant defensive traits are associated with higher diversification rates in plants. This study was one of the first to show strong support for Ehrlich and Raven's ideas, and remains a prominently cited empirical example (e.g. Agrawal & Konno, 2009; Coyne & Orr, 2004; Magallon & Sanderson, 2001; Schluter, 2000).

While Farrell et al.'s (1991) paper was an instant classic, major progress over the last three decades in the fields of plant molecular systematics, phylogenetic comparative methods and trait phenotyping warrants a reassessment of the role of latex and resin canals in plant diversification. Farrell et al. (1991) themselves stressed that their results were subject to future research, especially in regard to plant systematics (e.g. 'Plant phylogeny is the subject of intense current research, and all of the phylogeny estimates we accept should be regarded as possibly erroneous.'). Indeed, since Farrell et al.'s (1991) study, plant systematics has undergone major changes. Several notable milestones include the rise of molecular systematics, major updates to deep phylogenetic hypotheses, the development of 'big tree' methods and the formation of the Angiosperm Phylogeny Group (currently Angiosperm Phylogeny Group IV, 2016). While Farrell et al. (1991) argued that '...taxonomic error should be random with respect to the escalation-diversification hypothesis, making a significant effect harder to detect...', several of the original sister comparisons in the paper have changed dramatically under modern systematic analysis (see: Appendix S1; compare Tables S3 and S4). Thus, a re-assessment of the relationship between the latex, resin canals and plant diversification is now due.

Along with changes in molecular systematics, the last 30 years have also seen the development of novel phylogenetic comparative methods for evaluating links between trait evolution and shifts in diversification rates. New approaches for sister comparisons (Käfer & Mousset, 2014; Paradis, 2012) plus methods for explicitly modelling diversification rates (reviewed in Morlon, 2014; O'Meara & Beaulieu, 2016) offer benefits over the original sign test approach used by Farrell et al. (1991). For example, modern

sister comparison methods, such as diversity contrast tests, now consider the numerical values of species richness across clades (opposed to the qualitative sign of the difference only – as in sign tests) (Barraclough, Harvey, & Nee, 1995, 1996; Sargent, 2004; Wiegmann, Mitter, & Farrell, 1993). Modern sister-clade comparison methods also use maximum likelihood to estimate null hypotheses (McConway & Sims, 2004; Paradis, 2012) and to account for stem length biases (Käfer & Mousset, 2014). Given a well-resolved phylogeny, a collection of likelihood-based methods is also available to explicitly model lineage diversification through time (e.g. Alfaro et al., 2009; Pennell et al., 2014; Rabosky, 2014) sometimes simultaneously modelling trait evolution (e.g. Beaulieu & O'Meara, 2016; Maddison, Midford, & Otto, 2007). While these clade-based models come with their own set of assumptions, they provide a more robust framework to test for strong associations between the timing of trait evolution and shifts in diversification rates. Ultimately, modern methods can account for several limitations to the original sign tests and create opportunities to apply a set of complementary methods in tandem to evaluate patterns of diversification across multiple scales.

Here, we ask whether updated systematic, phylogenetic and phenotypic data crystallizes, complicates, or challenges the relationship between lineage diversification and the evolution of latex and resin canals. We test for macroevolutionary patterns consistent with the predictions from Ehrlich and Raven (1964) at multiple phylogenetic scales. First, we use expanded and updated sister clade comparisons to broadly test whether clades with canals are generally more speciose than clades without canals. Second, zooming in on two groups with more phylogenetic resolution and sufficient phenotypic sampling – the poppies (Papaveraceae) and the aroids (Araceae) – we use ancestral state reconstructions and phylogenetic models of lineage diversification rates to examine whether independent origins of latex and resin canals correspond to positive shifts in diversification rates. This integrative approach allows for a replicated, multi-scale test of the hypothesis that trait evolution is repeatedly associated with increased net diversification rates, while avoiding the drawbacks of studies that rely on any single scale or approach (see: Maddison & FitzJohn, 2014; Rabosky & Goldberg, 2015). Together, this study represents a modern test of the macroevolutionary consequences of latex and resin canals – evolutionarily convergent and ecologically important defensive traits in vascular plants.

2 | MATERIALS AND METHODS

To test for associations between latex, resin and lineage diversification rates, we (a) compiled an updated list of taxa reported with latex or resin canals in the literature, (b) conducted modern sister comparisons (across a broad set of clades) and (c) reconstructed historical patterns of diversification rates and trait evolution in two focal families from the sister comparisons that had higher data resolution. General methods for each approach are detailed below, with specific details available in the Supporting Information.

2.1 | Trait database

To improve accuracy from the original Farrell et al. (1991) sister comparisons and to expand our dataset to more broadly test the 'escape-and-radiate' hypothesis, we compiled current published information about the phenotypic distribution of species with and without latex and/or resin canals. First, we surveyed previously published datasets on the presence and absence of latex and resin canals, including those used by Farrell et al. (1991) (see Table S3), plus 76 additional sources. We focused on comprehensive datasets rather than single-species accounts. Because these traits (especially latex) are taxonomically informative for many plant groups, we scrubbed several taxonomic sources: (a) the Angiosperm Phylogeny Group website (<http://www.mobot.org/MOBOT/research/APweb/>, accessed May through October 2018), (b) a number of floristic and taxonomic treatments (Condit, Pérez, & Daguerre, 2010; Dicht & Lüthy, 2006; Evert, 2006; Haston & Condit, 2011; Kubitzki & Kadereit, 2004; Lewinsohn, 1991; Mabberley, 2017; Singh, 2016; Tomlinson, 2016; Willis, 1973), and (c) a compendium of plant resins (Langenheim, 2003). After data collection, we updated the list of taxa to represent current nomenclature using the R package *taxize* (Chamberlain & Szöcs, 2013), cross-referencing between the Taxonomic Name Resolution Service (TNRS) reference database and the National Center for Biotechnology Information (NCBI) taxonomy browser. For any taxon that disagreed across these two databases, and for any hits that had a score less than 100%, we manually checked Tropicos (Garden, 2003) for nomenclature. Finally, duplicate taxa were concatenated into a single datum, with more recent data supplanting older data.

2.2 | Sister clade comparisons: a broad test of the relationship between latex, resin canals and diversification rates

We used sister comparisons to perform a broad-scale test of the relationship between plant diversification and latex and resin canals. We combined our phenotypic database with recent literature on plant systematics and richness estimates (Table S4) to identify independent and up-to-date sister comparisons between sister-lineages with and without latex and/or resin. Sister comparisons were restricted to cases where: (a) monophyly was supported for each clade, (b) there was evidence for an independent origin of the latex and/or resin canals within the focal clade, and (c) there was a well-supported sister clade that entirely (or almost entirely) lacked the focal traits. Under these criteria we aimed to include as many comparisons as possible – including the 16 original comparisons (Table S3) performed by Farrell et al. (1991) as feasible. Due to shifts in taxonomy, two of the original comparisons could not be included (see Celastrales in Appendix S1, and compare Tables S3 and S4). Rather than having our analyses dependent on a single richness value per clade, we collected a range of minimum and maximum richness estimates, collected from the Angiosperm Phylogeny Group Website (<http://www.mobot.org/mobot/research/apweb/>, accessed September through October 2018), The Plant

List database (<http://www.theplantlist.org/>, accessed September through October 2018), and primary literature (Table S4).

To test whether clades with the latex and resin canals were more speciose on average than clades without these traits, we applied difference-based contrast tests (e.g. Paradis, 2012; Sargent, 2004). Our data were non-normally distributed, so we used a nonparametric Wilcoxon signed-rank test. We performed a one-sided, paired test to evaluate the hypothesis that richness is higher, on average, in canal-bearing clades relative to canal-lacking sister clades. This analysis was conducted once for our maximum richness estimates for each clade, and then repeated in an independent test using the minimum richness estimates. We performed each difference-based contrast test using the *wilcox.test* function in the R package *stats* (R Core Team, 2017), and cross-validated these results with the *diversity.contrast.test* function in the R package *ape* (Paradis, Claude, & Strimmer, 2004). Note that in order for sister comparisons with similar richness values to be included in these analyses, it was necessary to add a small amount of random noise using the *jitter* function in base R (R Core Team, 2017).

To make this study directly comparable to Farrell et al. (1991), we also applied the above methods to the original richness dataset of Farrell et al. (1991) (Table S3). This allowed us to evaluate whether any differences between our results and the results of Farrell et al. (1991) were due to updates made to statistical methods, phenotypic/phylogenetic datasets, or both. Because Farrell et al. (1991) occasionally reported a range of values for some clades, we analysed both their maximum and their minimum richness estimates in two separate contrast tests, performed as above.

2.3 | Models of lineage diversification rates: Zooming in on patterns of trait evolution and lineage diversification rate shifts

Although sister comparisons offer a powerful tool for replicated tests across a broad swath of clades, they do not evaluate whether the timing of diversification rate shifts in a phylogeny are associated with the evolution of a trait of interest. To evaluate more nuanced relationships between lineage diversification and the timing of trait evolution, we used MEDUSA analyses and ancestral state reconstruction in two plant families: poppies (Papaveraceae) and aroids (Araceae). Both groups showed patterns consistent with escape-and-radiate evolution in the sister comparisons – that is, greater species richness in canal-bearing clades (Table S4) – providing good candidate groups to test for linked evolution of the putative relationship between diversification and trait evolution. Defensive traits are also well documented for both of these groups: laticifers across Papaveraceae (Hoot, Wefferling, & Wulff, 2015) and laticifers and resin canals across Araceae (Cusimano et al., 2011; French, 1987, 1988).

We reconstructed relative time ultrametric maximum clade credibility phylogenies of each group using BEAST (Bouckaert et al., 2014). For details on phylogenetic reconstruction see the Supplemental Methods. We analysed lineage diversification rates of each clade using the R package MEDUSA (Alfaro et al., 2009; Brown, FitzJohn, Alfaro, & Harmon, 2018). To visualize the rate shifts, net

diversification rates and richness data on each family tree (Araceae or Papaveraceae), we plotted the bootstrapped results of MEDUSA diversification analyses onto the respective maximum clade credibility tree using the *plotMultiMedusa* function from the MEDUSA package (Alfaro et al., 2009; Brown et al., 2018). To examine whether shifts in lineage diversification were associated with the evolution of latex/resin, we conducted ancestral state reconstructions and plotted evolutionary gains and losses of latex/resin. Because we are uncertain about the link between these traits and diversification, we reconstructed trait evolution using both state-dependent diversification models and diversification-free models. Specifically, we used the *asr* function in the R package *diversitree* (FitzJohn, 2012) to reconstruct marginal likelihoods of ancestral states for discrete characters under a model of evolution (biSSE) that accounts for diversification, and the *rayDISC* and *corHMM* functions in the R package *corHMM* (Beaulieu, Oliver, & Beaulieu, 2017) to reconstruct ancestral states under a diversification-free model (canonical Markov model) (Lewis, 2001). Due to constraints of our dataset, we were not able to reliably make inferences using hiSSE or fiSSE analyses (see Supporting Information Methods). Finally, to summarize diversification rates over time and with respect to each character state, we adopted the approach of Nakov, Beaulieu, and Alverson (2018): we binned the phylogeny into time-intervals of 0.001 units, resampled the parameter estimates at each interval and then plotted the values by character state. Note that diversification rates are sensitive to the maximum tree depth and are inflated due to the relative time calibration in BEAST (Supporting Information Methods); however, this should not affect conclusions drawn within the clade.

3 | RESULTS

3.1 | Trait database

In total, we gathered data on the presence and absence of latex and resin canals across over 345 families and 986 genera of vascular plants (Table S1 is archived in the Dryad Digital Repository <https://doi.org/10.5061/dryad.2mn0j54>). Compared to previous databases (Lewinsohn, 1991; Metcalfe & Chalk, 1983), this expanded database increases the number of sampled groups by hundreds of additional genera and nearly 20 additional families. Plotting the data onto a phylogeny for vascular plants (Figure 1) illustrates wide sampling effort across the plant tree of life. However, there are several notable gaps in available information on the presence/absence of latex/resin canals across plant families, suggesting clades where research is lacking (e.g. several families in the orders Poales, Santalales, Asparagales and Brassicales; for more, see Table S2 and Appendix S1).

3.2 | Sister clade comparisons: A broad test of the relationship between latex, resin canals and diversification rates

In total, we identified and analysed 28 independent sister comparisons that fit our criteria (Table S4), nearly doubling the original

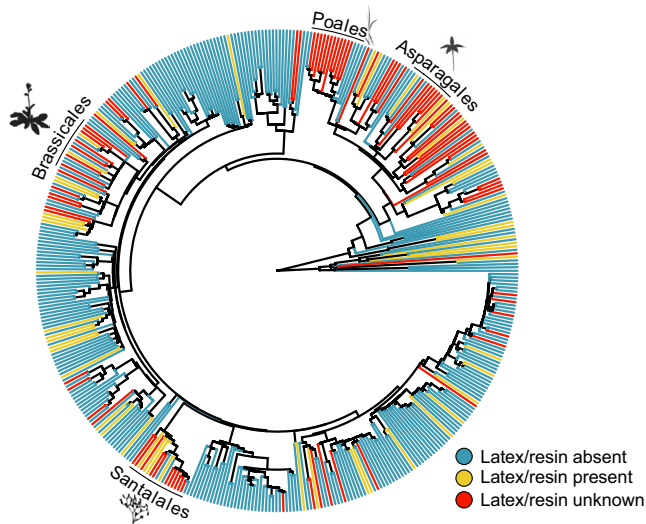


FIGURE 1 Family-level phylogeny (Zanne et al., 2014) showing the presence (yellow) or absence (blue) of latex or resin canals across plants. Branches in red indicate clades where the occurrence is unknown. Names denote plant orders for which missing data are particularly common (silhouettes are utilized from phylopic.org). Note that this figure does not indicate if traits are synapomorphic, but rather where data are available or lacking. A version of this figure with latex and resin canals depicted as independent traits can be found in the Supporting Information

sample size of Farrell et al. (1991) ($n = 16$, Table S3). Detailed information on each sister comparison, as well as notes on clades that did not fit all of the criteria but offer promise for future study, are detailed in Appendix S1. A Wilcoxon signed-rank test on our 28 sister comparisons suggested that latex/resin-bearing clades are not more species-rich than sister groups without these traits; this was true whether analysing minimum ($V = 250$, $\Delta\bar{x} = 1,132 \pm 4,655$ species, $n = 28$, one-tailed $p = 0.147$; Table S4) or maximum ($V = 245$, $\Delta\bar{x} = 1,519 \pm 6,303$ species, $n = 28$, one-tailed $p = 0.132$; Table S4) richness estimates.

Repeating our analysis on the original richness data from Farrell et al. (1991) (Table S3, indices 1–16) revealed that the differences between our results and the results of Farrell et al. are a consequence of additional trait data and updated systematics, not a consequence of updated analysis methods. Using the original dataset of Farrell et al. (1991), 13 of the 16 original comparisons under previous taxonomy had higher richness (sign test: 13/16, $p = 0.0106$; Table S3). When we apply modern contrast tests to the same dataset, we find an even stronger relationship, whether computed with Farrell's minimum richness values ($V = 120$, $\Delta\bar{x} = 1,980 \pm 5,512$ species, $n = 16$, one-tailed $p = 0.003$; Table S3) or maximum ($V = 119$, $\Delta\bar{x} = 1,799 \pm 5,467$ species, $n = 16$, one-tailed $p = 0.003$; Table S3), suggesting that our results are not due to methodological differences between studies. A box plot summarizing the results for (a) the original data in Farrell et al. (1991) and (b) our extended dataset, can be seen in Figure 2.

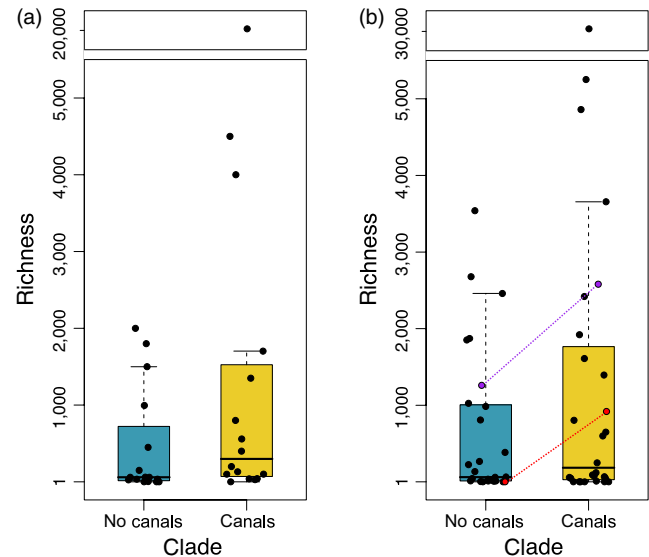


FIGURE 2 A box plot showing the distribution of species richness values across clades with latex/resin canals and their sister clades without canals from (a) Farrell et al. (1991) (Table S3) and (b) our updated and extended dataset (Table S4). In panel b, purple shows Araceae, while red denotes Papaveraceae, both of which we investigate in additional analyses. Note that the y-axes contain breaks, which have different upper values

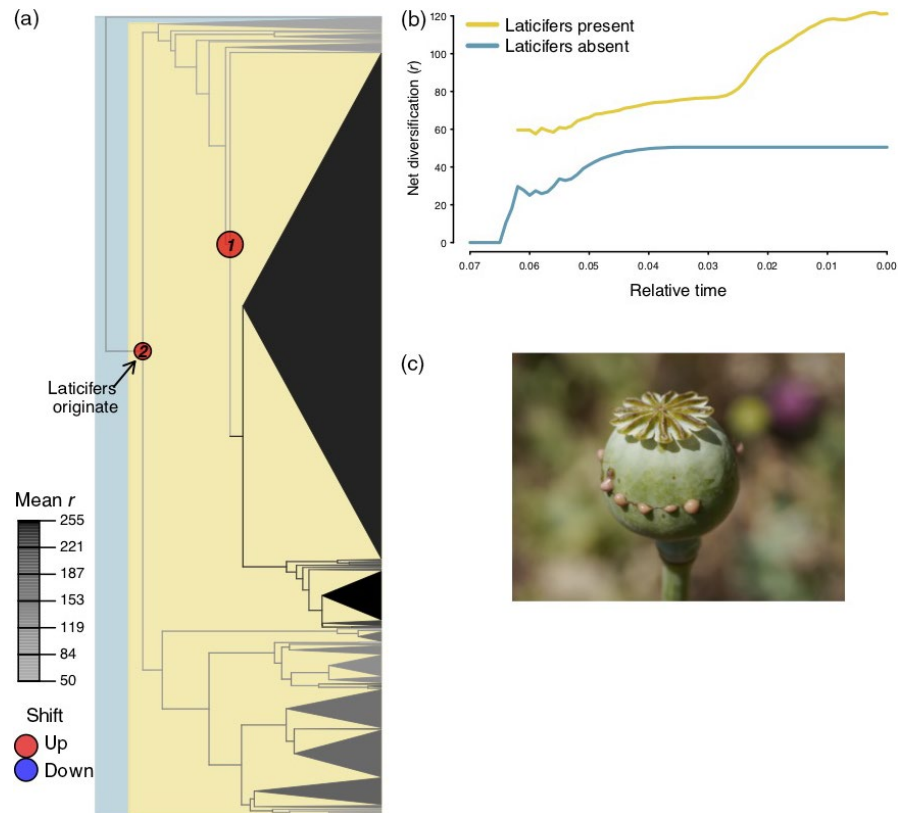
3.3 | Models of lineage diversification rates: Zooming in on patterns of trait evolution and lineage diversification rate shifts

For diversification analyses performed using MEDUSA, we present the results separately for each of the two focal families: first Papaveraceae and then Araceae. Note that in the sister comparisons, both Araceae and Papaveraceae met the predicted pattern of greater species diversity in canal-bearing clades (Table S4). Diversification rate shifts are discussed with respect to particular nodes, numbered based on the output of MEDUSA. This was done with the intent of allowing readers to lookup specific statistics in the Supporting Information. Lastly, ancestral state reconstructions for latex and/or resin inferred from *diversitree* did not differ qualitatively from reconstructions under a diversification-free Markov model – the character histories were the same across models. All reconstructions can be found in Figures S1–S4.

3.3.1 | Papaveraceae: the origin of laticifers is associated with a shift in diversification rates

Pairing marginal ancestral character reconstructions with MEDUSA models revealed that latex originated once in poppies (Papaveraceae), and that this origin coincided with a positive shift in the net lineage diversification rate (consistent with escape-and-radiate coevolution). Marginal ancestral state reconstructions revealed that laticifers originated once in Papaveraceae and were never lost subsequently (Figure

FIGURE 3 The results of MEDUSA diversification analyses in Papaveraceae. The results from 1,000 random samples of the posterior distribution are summarized on (a) the maximum clade credibility tree, showing the inferred shifts in mean diversification rates (r) and the origins of laticifers. (b) The estimated net diversification rates (r) through relative time for lineages with and without laticifers. (c) Rich, latex exuded by *Papaver somniferum* (Papaveraceae), near Chihuahua, Mexico (photo credit: Anurag Agrawal)



S1). We found no data suggesting resin canals in Papaveraceae. Pairing these analyses with MEDUSA revealed that laticifers originated early on in the group, and that this origin is associated with an increase in diversification rates and followed by a subsequent but unassociated diversification event nested within the laticiferous group (Figure 3a). The initial shift (node.id = 2; mean shift = 20.37 ± 19.24 ; Figure 3a; Table S5) represented a threefold rate increase in diversification, and occurred concurrently (on the same branch) with the evolutionary origin of laticifers, early on within the lineage, enveloping all extant poppy genera except for the non-laticiferous *Pteridophyllum*. The second and larger increase is nested deeper in Papaveraceae (node id = 1; mean shift = 176.33 ± 21.10 ; Figure 3a; Table S5). This more recent shift subtends most of the subfamily Fumarioideae, including the notably species-rich genera *Corydalis* (586 species) and *Fumaria* (57 species); however, the shift is not associated with any evolutionary gains or losses of laticifers (Figure 3a). Lastly, sampling the parameters through time for each phenotypic state reveals that net diversification rates are always higher in the laticiferous lineages, relative to the non-laticiferous lineage (*Pteridophyllum*) (Figure 3b).

3.3.2 | Araceae: the evolution of latex and resin canals does not correspond with shifts in diversification rates

While our analyses uncover an eventful history of diversification and trait evolution within Araceae, with laticifers evolving twice and resin canals evolving once within the family, there was no obvious

association between any of the three evolutionary origins of latex or resin and positive shifts in net diversification rates (Figure 4a). In total, MEDUSA estimated six rate shifts, four of which were negative (i.e. diversification slowing down; Figure 4a). Early on in the lineage, before latex or resin had evolved in the family (Figures S2–S4), diversification increased (node id = 2; mean shift = 105.86 ± 31.33 ; Figure 4a; Table S6). Following this initial increase in diversification, there were four subsequent decreases in diversification rates and one large increase in diversification that was 50 times the magnitude of the original increase (node id = 1; mean shift = $5,312.28 \pm 3,443.52$; Figure 4a; Table S6). Only one of the six total shifts corresponded to an evolutionary change in the focal traits: a gain of laticifers was associated with a 27% reduction in diversification rates (node id = 5; mean shift = -121.55 ± 101.70 ; Figure 4a; Table S6), the opposite of the prediction from escape-and-radiate coevolution. Similarly, following the origin of resin canals, a subsequent reduction in diversification rates was observed (node id = 6; mean shift = -119.60 ± 39.07 ; Figure 4a; Table S6). Lastly, sampling the rates through time for each phenotypic state illustrates that, despite no association between the timing of trait origination and diversification shifts, overall net diversification rates are still consistently higher when laticifers and/or resin canals are present in Araceae (Figure 4b).

4 | DISCUSSION

Testing for evidence of 'escape-and-radiate' coevolution has been a major goal in evolutionary ecology ever since Ehrlich and Raven

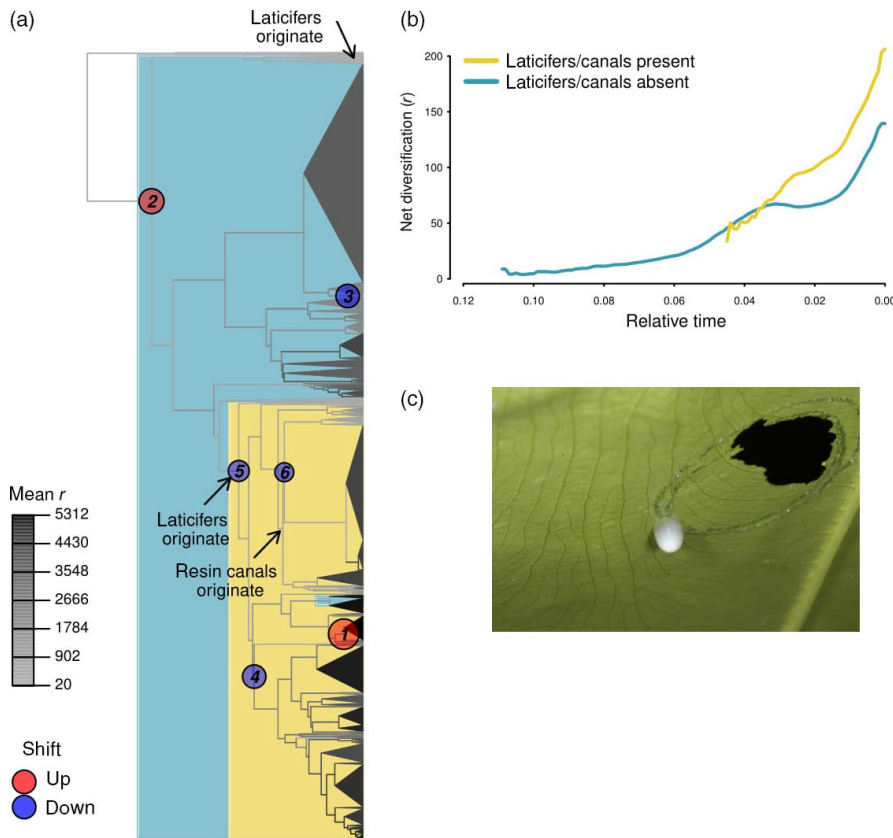


FIGURE 4 The results of MEDUSA diversification analyses in Araceae. The results from 1,000 random samples of the posterior distribution are summarized on (a) the maximum clade credibility tree, showing the inferred shifts in mean diversification rates (r) and the origins of resin canals and laticifers. (b) The estimated net diversification rates (r) through time for lineages with laticifers and/or resin canals and lineages without. (c) Latex exuding from a trenched leaf of *Colocasia gigantea* (Araceae), in Ba Be National Park, Vietnam (photo credit: Chris Darling)

published their 1964 hypothesis (Futuyma & Agrawal, 2009). In this study, we revisit a classic test of this hypothesis, Farrell et al.'s (1991) paper investigating whether the evolution of latex and resin canals spur lineage diversification in plants. We draw on an additional 28 years of systematic, phylogenetic and phenotypic resources to conduct a multi-scale reevaluation of this question (Farrell et al., 1991). We found poor support for the relationship between the evolution of latex and resin canals and enhanced diversification rates across scales. At a broad scale, sister-clade comparisons did not support the prediction of greater species richness in canal-bearing clades. At a finer scale, zooming-in on two clades (that were supported in the sister-clade analyses) using diversification rate analyses revealed that origins of canals were disconnected from the timing of diversification rate increases: while rates were higher overall when canals are present, of the four origins examined only one was associated with an increase in diversification rates. While our study does not rule out a conditional role of latex and resin in driving diversification in some groups, our findings do suggest that the evolution of latex and/or resin canals should not be invoked as a general, consistently replicable explanation for patterns of species diversity across plants. Below we (a) discuss the complementary findings of our sister-clade and clade-specific analyses, (b) consider the potential for latex and resin canals to be conditional drivers of diversification in plants, and (c) acknowledge important caveats of our study and highlight ways forward for future research.

4.1 | The complementary results of sister-clade and clade-specific diversification analyses in evaluating the latex/resin canal hypothesis

The power of diversification rate studies (both statistically and theoretically) is increasingly predicated on evolutionary replication (Donoghue & Sanderson, 2015; Maddison & FitzJohn, 2014). In this worldview, our ability to confidently assign a trait a causal role in driving increased diversification requires statistically significant replication. On the other hand, detailed studies within clades are required to link the timing of trait evolution with diversification dynamics, and detailed single (non-replicated) occurrences of a trait associating with high diversification rates have been cited as evidence for a role in driving patterns of diversity in several prominent examples (e.g. the evolution of flowers, mammary glands; Wagner & Lynch, 2010). Thus, while sister comparisons offer a broad view of diversification across plants, in-depth studies of diversification in focal clades are essential to understand the relationship (or lack thereof) between trait evolution and diversification. We contend a multi-scale approach marries the best of both worlds by allowing for more nuanced tests of relationships between traits and diversification, while not losing evolutionary replication as additional groups become well-resolved.

In our study, detailed modelling in two sister clades revealed a complex relationship between traits and the timing of diversification. In Araceae, we found a general disconnect between trait

evolution and the tempo of diversification. However, Araceae did show higher diversification rates in laticiferous and canal-bearing clades, suggesting that an underlying relationship should not be ruled out entirely. Indeed, it may be unrealistic to expect 'key innovation' traits to associate instantaneously (on the same branch of a phylogeny) with increased diversification rates in all cases due to the many confounding factors possible at the macroevolutionary scale (Rabosky, 2017; Vamوسي, Magallón, Mayrose, Otto, & Sauquet, 2018). In Papaveraceae, we found a clear concordance between the origin of latex and a positive shift in diversification, consistent with the *a priori* hypothesis. However, a closer look at the biology of this clade uncovers additional traits that arise at that same node as latex (e.g. calcium oxalate seed crystals) that could be associated with the diversification shift early on in the lineage. This suggests that there is as much evidence for latex as a 'synnovation' (Donoghue & Sanderson, 2015) as for a 'key innovation' in this group. These analyses demonstrate that closer examination of tractable clades from sister comparisons are a fruitful approach for uncovering nuanced effects of latex and resin canals on diversification. Pairing sister clade analyses with additional in-depth clade-based analyses as more data become available will be a particularly fruitful approach in future studies.

4.2 | Is there evidence for a conditional role of latex and resin in spurring plant diversification?

While we did not find a strong replicable relationship between latex and lineage diversification across plants, we cannot rule out a context-dependent relationship between diversification and the evolution of latex and resin canals. Our study thus joins a growing body of work suggesting that more theoretical and empirical work is needed to clarify how consistently and under what conditions hypothesized traits are expected to spur diversification, in coevolutionary (Yoder & Nuismer, 2010) and 'key innovation' frameworks (Rabosky, 2017). Because of their high level of evolutionary convergence across plants and their clear role in defense, latex and resin are a promising model trait to examine this topic in future studies.

Several other plant traits are hypothesized to conditionally spur diversification rates in plants, and these traits could be included in future analyses. For example, dioeciousness (Sabath et al., 2016) and mutualisms (Weber & Agrawal, 2014) are all hypothesized to impact lineage diversification in certain conditions. More directly, both the amount and chemical content of latex and resin vary considerably across species that have been investigated (Konno, 2011; Langenheim, 2003), and have been shown to impact the traits defensive efficacy (Agrawal, Lajeunesse, & Fishbein, 2008). As such, one might predict that latex/resin with particularly toxic secondary metabolites, high secondary metabolite diversity, or high secondary metabolite abundance would have larger impacts on a plants' ability to 'escape' herbivory, and consequently, impact the relationship between these traits and diversification. Similarly, variation in the evolutionary responses of herbivores, such as trenching behaviour and

host switching, could condition diversification under escape-and-radiate dynamics. Interestingly, seven of the sister-clade lineages in this study have canal-cutting herbivores reported (D. Dussourd, pers. comm.), and in all seven cases the lineage with canals has higher diversity than their sister group.

Extrinsic factors may also drive conditionality in the relationship between latex/resin canals and diversification. For example, variation in rates of diversification or trait evolution between temperate and tropical clades (e.g. Mittelbach et al., 2007; but see: Schluter & Pennell, 2017) could obfuscate patterns in our data if sister clades consistently differ in their regional associations. Previous work by Lewinsohn (1991) found that latex is more common and more abundant in tropical plant species and herbivory pressures have been shown to be higher in the tropics (Baskett & Schemske, 2018; Coley & Barone, 1996). A cursory post-hoc examination of the clades in this analysis, in which we evaluated whether sister clade status is confounded with tropicality, did not reveal a detectable signal of strong latitudinal differences across clades (Figure S5). However, a detailed analysis of diversification rates, latitude and trait evolution is necessary to fully disentangle this issue. In addition to latitude, other external factors hypothesized to impact plant diversification include ploidy, shifts in floral form and outcrossing (summarized in Table S3, Vamوسي et al., 2018). Ultimately, when evaluating patterns of diversification at such a large scale (across many independent origins of a trait), there is high potential for shifts in these traits to occur in at least some of the groups examined, potentially overshadowing the role of latex/resin in particular clades.

Finally, in studies that examine a large number of origins, accounting for clade age could prove informative. A high number of sister clade comparisons in our study were relatively young and species poor (Figure 2), which may confound our ability to detect diversification rate shifts. This is particularly true in light of recent evidence suggesting that diversification rates may be time-dependent across the tree of life (Henao-Diaz, Harmon, Sugawara, & Pennell, 2018). Ultimately, it may be that variation in the relationship between latex, resin and diversification rates across clades is unlikely to be explained by a single factor, or even handful of factors, and instead a myriad of clade-specific factors may shape diversification patterns across plants (Donoghue & Sanderson, 2015).

4.3 | Caveats of our approach and ways forward

Our study presents an updated test of whether latex and resin canals are broadly associated with increased diversification in plants. However, like that of Farrell et al. (1991), this study includes several major caveats that should be taken into consideration.

First, just as systematic relationships have changed in the 28 years, the relationships in this study may also change with future data and methodological advances. While this is a caveat of any phylogenetic study, it warrants particular mention in light of the differences between the 1991 paper and the current study. That being said, we have confidence in our data, as we only included sister comparisons with currently well-supported phylogenetic relationships.

However, to aid future work in this area, we discuss any uncertainty in the systematic relationships of our current sister comparisons, and identify clades we omitted, in Appendix S1.

Second, similar to phylogenetic hypotheses, updated trait data on the distribution of laticifers and ducts also have the potential to change future results. We attempted to take a conservative approach to aid in this issue, only making sister comparisons when the available trait data met certain criteria (i.e. laticifers and/or resin canals were known ancestral synapomorphies or derived states). However, for many potential sister-clades this was not possible due to insufficient trait or phylogenetic data (detailed in Appendix S1). While these instances were not analysed in this study, their inclusion in future analyses (with additional data) could alter conclusions. In a similar vein, if canal-bearing clades have higher persistence (over macroevolutionary time) than their canal-lacking sister clades, then it is possible that the extinction of lineages without canals could bias our results. If the 'true' sister clade has gone extinct, then the sister comparisons will be conducted on the next closest-related clade. A similar bias may exist if laticiferous or resinous clades go extinct and thus are not available to test. While these biases cannot be accounted for in most sister comparisons, they could be an issue, particularly for deep trait origins (like most origins of latex and resin canals), or for lineages that have low (or negative) diversification rates.

Third, diversification rate analysis methodology is changing rapidly, and more sophisticated analyses of trait-dependent diversification applied to clade-specific studies could illuminate our understanding of this question. We were unable to apply state-dependent diversification models (e.g. hiSSE, Beaulieu & O'Meara, 2016) to our analyses due to a lack of phylogenetic resolution and power (see Supporting Information Methods), and while our MEDUSA analyses offer an agnostic characterization of diversification patterns in these clades, diversification analyses with hiSSE (Beaulieu & O'Meara, 2016) and fiSSE (Rabosky & Goldberg, 2017) will more directly test the state-dependent hypothesis that diversification is dependent on latex and resin canals, as well as disentangle the effects of focal traits from the hidden effects of unmeasured drivers of diversification. These and other sophisticated methods will become increasingly accessible to researchers as more species-level phylogenies and trait data become available for clades representing independent origins of canals.

Fourth, our study (like Farrell et al., 1991) treats laticifers and ducts as a single, discrete character state and assumes that all laticifers and resin ducts play an equivocal role in defense. While we have evidence of defensive functions for laticifers and/or resin canals in many of the groups studied (Konno et al., 2004 [Caricaceae]; Konno et al., 2006 [Moraceae]; Dussourd & Eisner, 1987 [Apocynaceae]; Dussourd, 1993, 1995 [Asteraceae, Campanulaceae]; Kniep, 1905 [Euphorbiaceae]; Harris, 1960; Lewinsohn, Gijzen, Savage, & Croteau, 1991; Phillips & Croteau, 1999 [conifers]; Nawrot, 2017 [Papaveraceae]), not all occurrences of laticifers or resin canals have been tested for defensive roles. Given the variation in form (e.g. ideoblasts, sacs, canals, trichomes) and function (e.g. defense, pollinator attraction, etc.) of secretory structures containing latex and

resins, binning laticifers and resin canals into binary states may oversimplify the nature of these traits. Given that anatomical data are limited for the structure of laticifers and resin canals across clades (Farrell et al., 1991), and that the role of defense has not been tested in most occurrences of laticifers (Castelblanque et al., 2017), broader categorization is currently intractable in most clades. Furthermore, additional categories would increase the number of parameters in diversification models, further increasing the demand for more trait data. Because we were retesting a historically impactful study, and for the reasons outlined in Farrell et al. (1991) and Dussourd and Denno (1991), we make the assumption that latex and resin canals are a single defensive syndrome. Currently there is not enough data to test resin canals independently, but a cursory analysis considering latex separately reveals that relationship between latex and diversification is even weaker than when both traits are considered together ($V = 230$, $\Delta\bar{x} = 1,552 \pm 6,421$ species, $n = 27$, one-tailed $p = 0.1653$). However, future studies that are able to analyze these traits independently and incorporate trait variation within latex and resin canals will illuminate whether these traits show similar or different patterns in relation to diversification dynamics across plants.

5 | CONCLUSIONS

Here, we revisited a classic test of Ehrlich and Raven escape-and-radiate dynamics: an association between the evolution of defense exudates (latex and resin canals) and diversification rates across plants. Both at the broad scale (using updated sister-clade approaches across 28 clades) and at the narrower scale (modelling diversification rates and trait evolution in two clades that vary in latex/resin presence and absence), we find that the updated tests muddle the previously reported relationship between latex/resin evolution and diversification. Post-hoc analyses revealed that the change in results is due to updates to plant systematics over the last 28 years (not methodological advances in the statistical analyses or the addition of new data). The conclusions of this study, as those of the original study, are provisional and could change with updated phylogenies and trait data. We suggest that, while both theoretical and empirical work grounded in understanding conditionality in 'escape-and-radiate' dynamics may allow for more nuanced tests of the hypothesis in the future, there is currently not strong evidence for latex or resin as general, consistently replicable drivers of species diversity across plants.

ACKNOWLEDGEMENTS

We thank Anurag Agrawal and Michael Sanderson for substantial early feedback on this project. We are grateful to Jeremy Beaulieu for feedback on earlier analyses with *hisse* – even though these analyses did not make it into the final paper. Thank you to Keir Wefferling and Laura Lagomarsino for discussions on Papaveraceae and Araceae, respectively and to Eric LoPresti, Bruce Martin, Erika LaPlante, Isabela Borges, Ash Zemenick and

Cosmo for discussion and support throughout the project. We are grateful to Teofil Navov for sharing code that facilitated the production of Figures 3 and 4, and to Anurag Agrawal and Chris Darling for sharing their fantastic photos for use in those figures. The thoughtful comments from two anonymous reviewers greatly improved this manuscript.

AUTHORS' CONTRIBUTIONS

L.P.A. and M.G.W. conceived the ideas and designed the methodology; D.W.W.H. and M.R.F. performed literature review and constructed the trait database; M.R.F. and M.G.W. analysed the data and M.R.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The latex and resin canal data are deposited on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2mn0j54> (Foisly, Alberta, Hughes, & Weber, 2019). A list of data sources for this database, are referenced in shorthand within the database, and in full format in the 'data sources' section (below).

Foisly, M. R., Alberta, L. P., Hughes, D. W. W., & Weber, M. G. (2019). Data from: Do latex and resin canals spur plant diversification? Re-examining a classic example of escape and radiate coevolution. Dryad Digital Repository, <https://doi.org/10.5061/dryad.2mn0j54>

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How to cite this article: Foisy MR, Albert LP, Hughes DWW, Weber MG. Do latex and resin canals spur plant diversification? Re-examining a classic example of escape and radiate coevolution. *J Ecol.* 2019;107:1606–1619. <https://doi.org/10.1111/1365-2745.13203>