

Flammability and serotiny as strategies: correlated evolution in pines

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Fire may act as a selective force on plants both through its direct effects by killing or wounding susceptible individuals and through its effect on the environment: the post-fire environment may select specific physiological traits or life histories. We used phylogenetic independent contrasts to test the hypothesis that fire has selected for correlated evolution among alternative suites of traits in pines: a survival/avoidance suite characterized by thick bark, height, and self-pruning of dead branches; and a fire-embracing strategy in which plants invest little into survival, exhibit traits which enhance flammability, and use fire as a means to cue seedling establishment to the post-fire environment through serotinous cones. We created a set of alternative 'supertree' phylogenies for the genus *Pinus* from published sources. Using these alternative phylogenies, published ecological data for 38 pine species, and newly collected morphological data, we demonstrate that much variation in trait evolution occurs along a fire-surviving/fire-embracing axis. Pines vary in their susceptibility to ignition since a tree that retains dead branches is more likely to carry a fire into the canopy than a tree that self-prunes. The evolution of increased flammability may have altered evolutionary trajectories prompting an evolutionary switch from a fire-surviving to a fire-embracing life history. Alternatively, the fire-embracing strategy may in fact select for increased flammability to ensure canopy ignition and the realization of serotinous seed-release.

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Many plant species occupy habitats that experience regular wildfire. Plants exhibit adaptive responses to the direct effects of fire and there may also be selection for specific physiological or life history strategies in the post-fire environment. Several categories of plant traits are related to fire: traits that improve above-ground survival during fire, those that affect seedling or re-sprout fitness in the post-fire environment, and those that cue seedling establishment to the preferred environment. Fire-related traits that promote survival include thick protective bark and resprouting from underground storage organs (Keeley 1992a, b, Lopez Soria and Castell 1992, Moreno and Oechel 1993, 1994, Ostertag and Menges 1994, Jackson et al. 1999). Traits such as heat or smoke-stimulated seed germination and serotiny cue seedling establishment to the post-fire envi-

ronment (Went et al. 1952, Keeley et al. 1985, Kelly and Parker 1990, Keeley 1991, Lamont and Witowski 1995, Tyler and D'Antonio 1995, Tyler 1996, Keeley and Bond 1997, Keeley and Fotheringham 1997, 1998). We would expect traits favored in the early-successional environment, such as high growth rates and short leaf lifespan (Bazzaz 1979) or drought-tolerance traits (Williams et al. 1997), to be associated with post-fire seedling establishment.

In addition, the observation that some plants depend upon regular wildfire for their continued persistence and that many of these plants are quite flammable prompted Mutch (1970) to suggest that such plants might have evolved characteristics that enhance flammability and thereby prevent the invasion of less flammable, fire-sensitive species. Although this hypoth-

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esis has received a good deal of criticism (Snyder 1984, Troumbis and Trabaud 1989, Bond and Midgley 1995), recent theoretical work has emphasized the likely interactions between flammability traits and fire-related traits such as seedling fitness in the post-fire environment (Bond and Midgley 1995, Kerr et al. 1999). These studies demonstrate that the converse of Mutch's hypothesis is likely to be true – that is, where flammability-enhancing traits have evolved, plants are likely to evolve regeneration traits in response to the increased probability or intensity of fire. This gene interaction mediated through the environment has been labeled “niche construction” (Laland et al. 1996, Odling-Smee et al. 1996).

One of the most important plant properties that affects a plant's flammability is the retention of dead branches. Live fuels usually act as a heat sink during combustion until the moisture has been driven out of them: since the moisture content of dead wood is low, combustion of dead fuels drives the moisture out of living fuels (Bond and van Wilgen 1996). In pines, flammability is influenced by the self-pruning of dead branches: non-self-pruning pines are more likely to carry fire to their own canopy and to their neighbors, provided that they inhabit dense enough stands to carry canopy fire. In contrast, self-pruning of dead branches in pines has been interpreted as a means of prohibiting ground fire from spreading to the canopy. The size, shape and arrangement of plant parts also have strong effects on combustibility. Thin terminal twigs and low needle density, by increasing fuel surface area to volume ratios and by altering the fuel packing ratio (Rothermel 1972), are likely to influence ignition temperature and combustibility. Experimental work, however, is needed to test and quantify this effect.

Pines can exploit fire-prone environments through reproductive and vegetative traits. Serotiny (i.e. cones which require fire heat to release their seeds; but see Lamont et al. 1991), the ability to resprout, and thickness of protective bark are all fire-related traits that vary within the genus *Pinus* (Perry and Lotan 1979, Givnish 1981, Govindaraju 1984, McCune 1988,

Knight 1991, Lamont et al. 1991, Knight et al. 1994, Keeley and Zedler 1998, Jackson et al. 1999). The ecological implications of such traits cannot be viewed in isolation; these characteristics interact with one another, other morphological and life history traits, and the environment. Trade-offs among interacting traits can result in a pattern of correlated evolution, generating distinct suites of characteristics in species of different life histories or habitats. Such constellations of traits have been confirmed for leaf function, shrub and tree canopy architecture and leaf morphology (e.g. White 1983, Givnish 1986, 1987, Midgley and Bond 1989, Reich et al. 1997, Ackerly and Donoghue 1998).

Keeley and Zedler (1998) recently presented a framework for understanding ecological strategies in pines based on variations in site productivity and fire. They posited that pines can be categorized according to several different life history strategies. The relative success of these strategies is determined by the climate, productivity, and fire regime of the pine's habitat. We test if these strategies are reflected in suites of co-evolving traits and if serotinous pines represent a strategy which is associated with traits likely to increase plant flammability. We predicted two suites of correlated fire traits (Table 1): (1) a fire-embracing suite that would include serotiny, thin bark, short height, lack of self-pruning, relatively young mature age, more flammable foliage (less dense needles and smaller twigs) and limited seed dispersal (Keeley 1991); (2) and a fire-surviving strategy that would include no serotiny, thick bark, self-pruning, large mature height, older age at maturity, less flammable foliage and possibly resprouting and long-distance dispersal.

We then used phylogenetic comparative methods to investigate whether the suites of correlated traits observed in extant taxa have resulted from underlying patterns of correlated evolutionary changes. Most studies of correlated traits have examined either species within a particular community or, if related species were examined, have not formally included phylogenetic information in comparative analysis (e.g. White 1983, Givnish 1987, Keeley and Zedler 1998). Pheno-

Table 1. Predicted effects of fire-relevant traits on a survival strategy and a fire embracing strategy. ‘+’ denotes a positive effect, ‘-’ a negative effect, ‘0’ no likely effect and ‘?’ denotes uncertainty.

Character	Fire survival strategy	Fire embracing strategy	
		Effect on flammability	Effect on seedling regeneration following adult mortality
Mature height	+	-	0
Resprouting	+	0	?
Serotiny	0	0	+
Self-pruning of dead branches	+	-	?
Seed dispersal	+	0	-
Late reproduction	+	0	-
Thick bark	+	0	-
Needle density and/or twig thickness	+	-	?

typic correlations observed among species may or may not represent historical patterns of correlated evolution. Divergence in deep nodes can create strong correlations among traits in extant taxa even if the correlations in the underlying evolutionary changes are weak (Felsenstein 1985) or deep divergence can mask subsequent correlated evolutionary change such that correlations among traits in extant taxa are weakened (Ackerly and Donoghue 1998, Ackerly 1999). There has been growing attention to explicit tests of correlated trait evolution based on patterns of character variation and information on the phylogenetic relationships among species (e.g. Harvey and Pagel 1991). Felsenstein's (1985) method of independent contrasts provides a powerful quantitative tool to test for correlated evolutionary change in continuous traits (Garland et al. 1992, Pagel 1993).

Pinus offers an excellent opportunity to test for the evolutionary effect of fire on the interaction of flammability and fire survival or seedling recruitment traits since it appears that one entire subgenus of pines, subgenus *Strobus*, has few species that inhabit fire-prone environments. Subgenus *Strobus* thus offers a "control clade" so that we can test how the evolutionary patterns of correlated evolution differ between a fire and a non-fire clade. This study addresses the following questions: (1) Are traits likely to affect flammability (e.g. self-pruning, needle density) associated with fire-surviving vs. fire-embracing strategies? (2) Are the interspecific correlations among ecological traits the result of correlated evolutionary change along a fire-surviving/fire-embracing life history axis? (3) Do the evolutionary relationships among these traits differ among species in subgenus *Pinus* and *Strobus* and in the genus as a whole? (4) How robust are our results with respect to uncertainty in the phylogeny?

Methods

Comparative data and interspecific trait correlations

We used published comparative data available in Keeley and Zedler (1998), Kozłowski (1973), and McCune (1988) and data we collected from herbarium specimens at the California Academy of Sciences Herbarium and the University of California Berkeley Herbarium. The characters used in this study were mature height, minimum reproductive age, cone length, seed wing length, seed weight, relative resprouting ability, relative serotiny, bark thickness at maturity, relative self-pruning ability, twig thickness, needle length, and needle density (Table 2). Serotiny and self-pruning were scored following Keeley and Zedler (1998). Serotiny here is defined as the reten-

Table 2. Summary and descriptive statistics of ten ecological characters used in this study. Characters other than scored characters that were significantly non-normally distributed (Kolmogorov-Smirnov test, $p < 0.05$) were log-transformed for all analyses. Characters followed by (L) were log-transformed before analyses.

Character	Units	Min.	Max.
Mature height	m	8	71
Resprouting ability	score 1–10	1	10
Serotiny	score 1–10	1	10
Self-pruning ability	score 1–10	1	10
Seed dispersal	cm ² /g	0.0	0.84
Min. reproductive age (L)	years	3.5	60
Bark thickness (L)	cm	0.97	7.6
Needle length (L)	mm	21.9	245
Twig thickness (L)	mm	2.34	13.5
Needle density (L)	needles/cm	12.9	100

tion of seeds in persistent cones: lower values indicate no or short-term persistence and the highest values are for species which release seed only following fire. Polymorphic species were conservatively scored as intermediate values. Twig thickness, needle length, and needle density were measured from herbarium specimens. We measured twig thickness at the point on a primary shoot below which more than half the needles on the branch had been abscised. Needle density is the number of needles per cm of branch length. Seed wing length and seed weight were used to estimate potential seed dispersal ability according to the formula: dispersal = winglength²/seed weight (Anderson 1991, Benkman 1995). Trait values for herbarium data were averages of five to eleven specimens per species. Our analysis included data for 38 species of *Pinus* (Appendix I).

We predicted two suites of co-evolved fire-related traits: a fire-embracing and a fire-surviving suite. To minimize the number of pairwise comparisons among traits (Table 2), we chose three a priori 'anchors' for these suites of characters: self-pruning, bark thickness, and serotiny. Self-pruning ability is the most obvious trait that is likely to affect flammability, and bark thickness and serotiny are representative of the two hypothesized strategies, fire-surviving and fire-embracing. The Pearson correlation coefficient was calculated from the species data without considering phylogeny as a descriptive statistic to measure trait correlations among contemporary taxa (species correlation, R_{spec}). These three traits were tested against one another as well as against minimum reproductive age, mature height, needle length, needle density, twig thickness, seed dispersal and resprouting ability. We specified the direction of the predicted relationship (positive/negative) to allow one-tailed significance testing and used sequential Bonferroni correction to maintain table-wide $\alpha = 0.05$ error levels (Table 3).

Table 3. Significant pairwise evolutionary contrast correlations for all pines and for subgenus *Pinus* alone. No pairwise correlations were significant in the non-fire-prone clade subgenus *Strobus* excluding *P. lambertiana* and *P. strobus*, so the results are not listed here. Listed are evolutionary correlation coefficients (R_{pic}) and species correlation coefficients (R_{spec}). Analyses were carried out over 351 (subgenus *Pinus*) and 409 (all pines) alternative phylogenies and the number of alternative trees for which the correlation was significant is reported below. (*) indicates a significant species correlation. Comparisons are ordered from highest to lowest magnitude of R_{spec} for subgenus *Pinus*. (*) Indicates significant R_{pic} after Bonferroni correction.

Character 1	Character 2	Prediction	Subgenus <i>Pinus</i> , 27 species (pines that experience fire)			All pines, 38 species		
			R_{spec}	R_{pic} (min, median, max)	No. of sig. trees of 351	R_{spec}	R_{pic} (min, median, max)	No. of sig. trees of 409
Serotiny	Self-pruning	-	-0.743*	-0.706 -0.647 -0.557	351	-0.390	-0.566 -0.512 -0.419	396
			0.646*	0.492 0.594 0.686	326	0.725*	0.629 0.684 0.742	409
Serotiny	Log of needle length	-	-0.645*	-0.633 -0.613 -0.522	336	-0.095	-0.536 -0.507 -0.419	387
			-0.571*	-0.510 -0.428 -0.332	0	-0.632*	-0.318 -0.239 -0.149	35
Serotiny	Log of twig thickness	-	0.548*	-0.555 -0.483 -0.366	23	-0.351	-0.461 -0.399 -0.302	13
			-0.524*	-0.552 -0.486 -0.366	16	-0.553*	-0.466 -0.408 -0.318	14
Self-pruning	Log of needle density	+	0.524*	0.225 0.425 0.560	0	0.030	-0.037 -0.118 -0.226	0
			0.520*	-0.155 -0.020 0.087	0	0.179	-0.222 -0.126 -0.041	0
Self-pruning	Mature height	+	0.427	0.185 0.367 0.521	0	0.533*	0.384 0.490 0.580	343
			0.360	0.084 0.223 0.285	0	0.477*	0.153 0.249 0.304	0
Log of bark thickness	Mature height	+	0.305	0.092 0.303 0.445	0	0.477*	0.386 0.507 0.586	358

Phylogenetic trees

To test for correlated evolution among the traits of interest, a phylogenetic hypothesis for the genus was required. We conducted a "supertree" analysis of published pine phylogenies to obtain a set of alternative phylogenies. We used the Baum (1992) and Ragan (1992) method to combine phylogenies available in Wheeler et al. (1983), Conkle et al. (1988), Millar et al. (1988), Karalamangala and Nickrent (1989), Strauss and Doerkson (1990), Govindaraju et al. (1992), Malusa (1992), Wang and Szmidt (1993), Krupkin et al. (1996), Adams and Jackson (1997), Bergmann and Gillet (1997), Kaundun et al. (1997), Liston et al. (1999), and Wang et al. (1999). Coding of the subtree topologies resulted in a large character matrix that was analyzed using parsimony in PAUP 4 (Swofford 1993). 50 random starts were conducted and ten of these resulted in most parsimonious trees. 500 equally parsimonious trees were saved from each of these random starts, resulting in a total of 5000. Tree distance measures indicated that these 5000 phylogenies include representatives from three major islands of similar topologies. PAUP 4 settings: Optimality criterion = maximum parsimony, starting trees obtained via stepwise addition, starting seed on first replicate = 334850031, branch-swapping algorithm = TBR, zero-length branches not collapsed. These phylogenies were then pruned down to the 38 taxa for which we had character data and duplicate phylogenies were eliminated. All subsequent analyses were carried out separately for each phylogeny in the resulting set of 409 alternative topologies. In analyses of subgenera *Pinus* and *Strobos*, these phylogenies were further pruned down and duplicates again removed resulting in 351 different phylogenies for subgenus *Pinus* and three different phylogenies for *Strobos*. Our nomenclature follows Price et al. (1998), except that we include *P. quadrifolia* Parlatores ex Sudworth, although Price et al. consider it to be a hybrid between *P. juarezensis* and *P. monophylla*. NEXUS files containing all 5000 phylogenies and a strict consensus are available online at http://www.stanford.edu/~schwilk/research/data_page.html.

Calculation of independent contrasts

We calculated phylogenetic independent contrasts (Felsenstein 1985) to test for patterns of correlated evolutionary change among pairs of traits. To meet assumptions of parametric statistics, independent contrasts are usually standardized by dividing them by the standard deviation of the expected amount of change along each branch (Garland et al. 1992). Since our supertree pine phylogeny lacked branch length information, we report results assuming equal branch lengths to

minimize type I error rates (Purvis et al. 1994, Ackerly 2000).

Evolutionary contrast correlations

We used the same set of pairwise correlations for independent contrasts that we used for correlations of species trait values. To test for sensitivity to phylogenetic structure, we carried out these calculations over all 409 alternative phylogenetic trees for the entire data set, and then separately for the two basal clades that correspond to the *Pinus* (351 distinct phylogenies) and *Strobos* (three distinct phylogenies) subgenera to test how these relationship change in a clade that has species that inhabit fire-prone environments (*Pinus*) and one that in general does not (*Strobos*). As serotiny and resprouting do not vary in *Strobos*, we replaced serotiny with minimum reproductive age as one of the three anchor traits.

To test for correlated evolution between pairs of traits, correlations of independent contrasts (R_{pic}) were calculated using a correlation analysis forced through the origin (see Garland et al. 1992). Tree pruning and comparative analyses were carried out on new software written for this purpose; a version of this software, CACTUS 1.1 (Schwilk 1999), is available. Independent contrast analyses were carried out for each of the 409 alternative phylogenies.

Principal components analysis

We used principal components analysis of independent contrasts to identify the pattern of multivariate correlated evolution among traits. This analysis was carried out separately for each of the 409 alternative phylogenies. The loadings for the factor matrix were used to identify the suites of co-evolving characters for the entire data set over each phylogeny.

Results

Interspecific trait correlations

Over all pine species, six of the 24 pairwise correlations of species trait values were significant after sequential Bonferroni correction: self-pruning vs log of bark thickness, serotiny vs log of minimum reproductive age, self-pruning vs mature height, serotiny vs log of needle density, log of bark thickness vs mature height, and self-pruning vs log of needle length (Table 3). When the analyses only include pines in the subgenus *Pinus*, which make up the bulk of the fire-prone pines, three of these correlations were insignificant after Bonferroni correction, self-pruning vs mature height, self-pruning

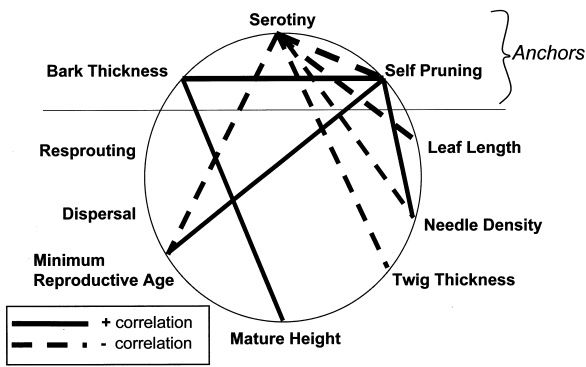


Fig. 1. Significant pairwise species trait value correlations for subgenus *Pinus*. Solid lines indicate significant positive correlations after a sequential Bonferroni correction. Dashed lines indicate significant negative correlations and line thickness indicates the relative strength of the relationship. To preserve power, we only tested all pairwise correlations among the anchor traits (bark thickness, serotiny and self-pruning) and between each anchor trait and the other seven traits.

vs log of needle length and log of bark thickness vs mature height. However, four additional correlations were significant in the direction predicted: serotiny vs self-pruning, serotiny vs log of needle length, serotiny vs log of twig thickness, and self-pruning vs log of minimum reproductive age, (Table 3, Fig. 1). Two pairwise correlations were significant in the subgenus *Strobus* subset: Bark thickness vs mature height ($r^2 = 0.788$) and self-pruning vs bark thickness ($r^2 = 0.914$). Both of these correlations, however, were not significant when the two fire-prone species, *P. lambertiana* and *P. strobus*, were removed from the data set.

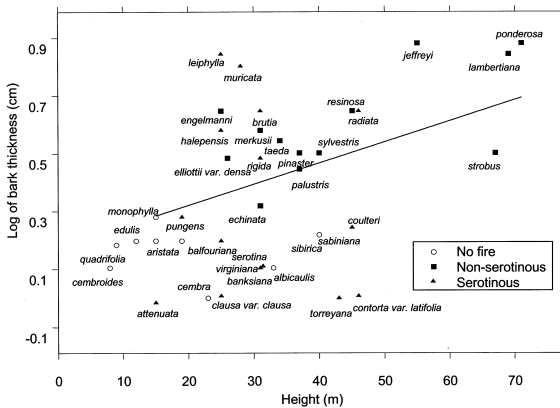


Fig. 2. Mature height versus bark thickness for 38 species of pines. Open circles are species that inhabit environments that do not experience fire, triangles are serotinous species and squares are non-serotinous species that inhabit fire-prone environments. The subgenus *Strobus* consists of all the open circles as well as *P. lambertiana* and *P. strobus*. A serotiny value of one or greater was coded as present. Regression line drawn is least-squares fit for data from all species that inhabit fire-prone environments (e.g. subgenus *Pinus* plus *P. lambertiana* and *P. strobus*) ($R^2 = 0.227$, $P = 0.0030$).

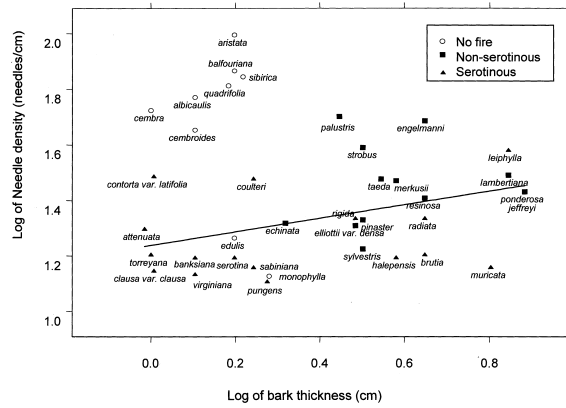


Fig. 3. Bark thickness and needle density values for 38 species of pines. Symbols are as described for Fig. 2. Regression line drawn is least-squares fit for data from all species that inhabit fire-prone environments (e.g. subgenus *Pinus* plus *P. lambertiana* and *P. strobus*) ($R^2 = 0.167$, $P = 0.028$).

An investigation of the species trait values shows that the relationship between bark thickness and height (Fig. 2) and that between bark thickness and needle density (Fig. 3) hold only for taxa inhabiting fire-prone environments and do not hold for either subgenus *Pinus* or *Strobus* alone.

Discrete trait analyses

The set of equally parsimonious phylogenies resulting from supertree construction was used in all evolutionary analyses. Pruned down to taxa for which we have species trait data, this set comprised 409 topologically distinct phylogenies (consensus tree shown in Fig. 4). Mapping fire-habitat type on the pine phylogeny showed that the basal divergence between the *Pinus* and *Strobus* subgenera was also a divergence into pines that generally inhabit fire-prone systems (*Pinus*) and those that generally do not (*Strobus*).

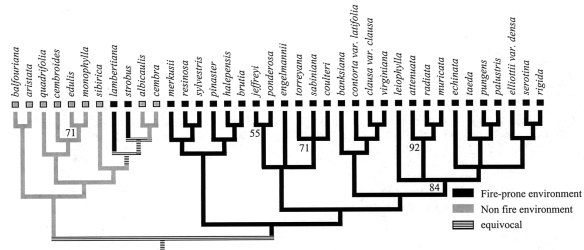


Fig. 4. A majority rule consensus of 409 phylogenies for 38 species of *Pinus*. This tree is for illustration only and analysis was carried out over all 409 alternative topologies. These phylogenies are the result of pruning the 5000 phylogenies down to the 38 taxa of interest and then eliminating duplicate topologies. Numbers indicate the percentage of phylogenies that supported the node above. Nodes with no numbers were supported by all 409 phylogenies. Parsimony reconstruction of fire-habitat type demonstrates the divergence between species that inhabit fire-prone environments and those that do not.

Pairwise evolutionary contrast correlations

Five of 24 pairwise independent-contrast correlations were significant over more than 50% of the 409 alternative phylogenies after sequential Bonferroni adjustments and the sign of all significant correlations matched our predictions: serotiny vs self-pruning (negative), self-pruning vs bark thickness (positive), serotiny vs needle length (negative), self-pruning vs mature height (positive), and bark thickness vs mature height (positive) (Fig. 5). Bark thickness vs mature height and self-pruning vs mature height were not significant in the subgenus *Pinus* subset. Two correlations were significant over three of the phylogenies for subgenus *Strobos*: bark thickness vs mature height and self-pruning vs bark thickness. Again, neither of these two correlations were significant when the two fire-prone species in our set of subgenus *Strobos* pines, *P. lambertiana* and *P. strobus*, were excluded from the analyses.

Principal components analysis

Principal components analysis of independent contrasts allows a distilled view of the patterns of correlated evolution among many characters. The first and second components of the PCA explained 34% and 17% of the variation in the independent contrasts for the ten traits. The variation explained by each axis and the loadings for each of the ten characters were very consistent across the 409 alternative phylogenies. Figure 6 shows the mean (± 1 SD) loading value for each of the traits on the first two components. The first component reflects the hypothesized continuum of fire life history traits and shows the strong correlation between bark thickness, mature height, self-pruning and minimum

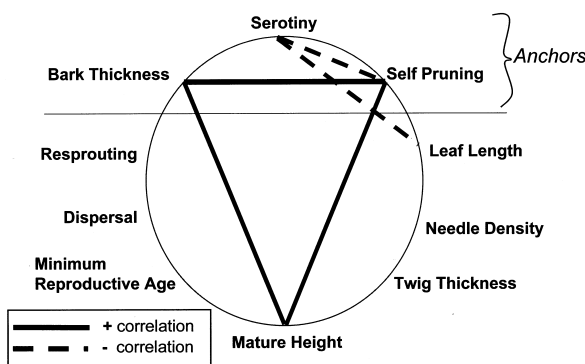


Fig. 5. Significant pairwise evolutionary contrast correlations for all pines, subgenus *Pinus*, and subgenus *Strobos*. Solid lines indicate significant positive correlations over more than 50% of the alternative phylogenies after a sequential Bonferroni correction. Dashed lines indicate significant negative correlations and line thickness indicates the relative strength of the relationship. To preserve power, we only tested all pairwise correlations among the anchor traits (bark thickness, serotiny and self-pruning) and between each anchor trait and the other seven traits.

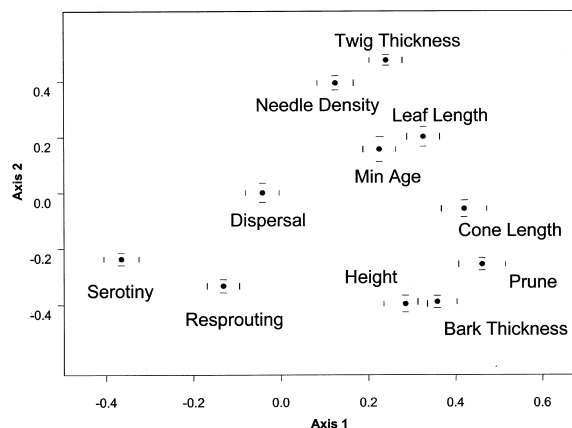


Fig. 6. Arrangement of 10 traits along the first two principal component axes constructed from independent contrasts. Points represent the mean factor loading from separate analysis over 409 equally parsimonious phylogenies; error bars indicate ± 1 SD.

reproductive age. These fire survivor traits were negatively associated with serotiny. Serotiny was also negatively associated with needle density, twig thickness and needle length. Seed wind dispersal ability shows no strong association with any other trait other than perhaps a negative association with minimum reproductive age. Resprouting, which we would expect to be associated with other fire-survival traits, instead is associated with serotiny.

Variation in the second principal component axis occurs mostly in the non-serotinous end of the first axis. This axis appears to separate evolution towards fire survival (thicker bark, taller height, self-pruning) from evolution towards and within the non-fire-prone pinyon and high altitude pines, which have thin bark, lower height, slow growth and later reproductive maturity.

Discussion

The results of independent contrast analysis confirm a constellation of correlated fire life history traits in *Pinus* that correspond largely with the predictions of recent theoretical considerations (Kerr et al. 1999, Schwilk unpubl.) and the results of Keeley and Zedler's analysis (1998). The correlations involving bark thickness were weaker in the subgenus *Pinus* than among all 38 taxa (Table 3); the subgenus *Strobos* showed a strong correlation between self-pruning and bark thickness, but this association becomes insignificant when the two fire-prone species in the subgenus, *Pinus strobus* and *P. lambertiana*, are removed from the analyses. Although subgenus *Strobos* has fewer taxa and therefore provides less power to detect significant correlations, the lack of significant correlations in the non-fire-prone species

supports the hypotheses that these suites represent ecological strategies related to fire.

The prediction that the fire-recruiting, serotinous strategy should be correlated with limited dispersal, was not borne out by this analysis. These results fail to show any correlation between dispersal and traits in the fire suite. Our rough estimate of wing area over seed weight likely serves as a poor proxy for dispersal ability. Most importantly, this estimate only takes into account wind dispersal – in most of the pines with wingless seeds, seeds are dispersed by birds rather than by wind. In this data set, many of the long-lived pines that live in fire-free environments have wingless seeds, and therefore are scored as zero dispersal although many have bird-dispersed seeds.

In a recent study investigating the allometry of bark thickness in *Pinus* as a defense against fire, Jackson et al. (1999) found that investment in thick sapling bark was common in species that experience short fire-return intervals while thin bark in saplings was associated with long fire-return interval habitats. This study presented and tested a theory that predicts differing defense allocation strategies in different environments using phylogenetically robust methods. However, by assigning pines to habitat categories that confound environment and the life history traits of the plants themselves (e.g. “Fire-resilient monospecific forest”), Jackson et al. fail to explain patterns that become understandable when traits such as serotiny and self-pruning are taken explicitly into consideration. The groups of pines with the highest bark allometry coefficients (relatively low sapling investment to bark) in the Jackson et al. study were pines in the subgenus *Strobus* and the least-self pruning serotinous pines in subgenus *Pinus*. These correspond well to the thin-bark pines in this study (Figs 4, 5). Jackson et al. attribute thinner sapling bark in longer fire-return interval habitats to increased competition for light. The desert and high altitude pines in *Strobus* and the post-fire regenerating serotinous pines, however, both experience relatively high light environments as saplings. Differences in bark thickness seem more easily interpreted in terms of differences in flammability and the probability of crown fire. Lack of investment in thick bark is likely a result of rare exposure to fire in the case of pinyon and high-altitude pines and selection not to invest in a defense ineffective against crown fire in the serotinous non-pruning pines.

Fire is unlikely to be the sole architect of these trait correlations. Selection in a fire-prone environment may bind additional characters to already correlated co-evolving suites. It is likely that any trait that increases fire intensity or the probability of crown fire is likely to make a fire-survival strategy less viable. Keeley and Zedler (1998) plausibly suggest that lower site productivity, by lowering maximum plant height, can increase the probability of crown fire and therefore select for serotiny. Selection that changes self-pruning or canopy

fuel packing could also influence the evolutionary trajectory of a whole suite of traits. Results of the independent contrast analysis show that evolutionary decreases in bark thickness have been correlated with decreases in self-pruning (Table 3, Fig. 4). Self-pruning is certain to have a strong effect on the probability of fire reaching the canopy and therefore killing the tree regardless of bark thickness near ground level. The significance of the other traits we studied that may affect flammability, however, is less clear. If needle density affects flammability, then a decrease in needle density, which could arise from faster growth rates leading to greater internode distance, could make plants more flammable and the fire-survival strategy less viable. Needle length, needle density, and twig thickness, however, are likely to be allometrically linked through biomechanical constraints. Needle density and twig thickness are likely to have the most obvious effects on flammability by altering the air/fuel mix. Needle length exhibits a negative evolutionary correlation with serotiny. Pine needle length may play a dual role in plant flammability: longer needles possibly act as a heat sink and retard flammability while on the tree, but the longer needles pack less efficiently as litter and may create a more flammable dry leaf litter layer which is likely to encourage a ground-fire regime (Robertus et al. 1989, Fonda et al. 1998).

The relationship between serotiny and needle length is especially interesting since the independent contrast correlation was significant, while the species correlation was not. Differences between species correlations and independent contrast correlations are strongest when the traits are most conserved (Ackerly and Donoghue 1998, Ackerly and Reich 1999). It is not surprising, therefore, that serotiny and needle length are the least convergent characters in this data set and have the lowest quantitative convergence index values (Schwilk unpubl.). The significant contrast correlation indicates that despite a great deal of variation in needle length within both serotinous and non-serotinous species, evolutionary increases in serotiny have been associated with decreases in needle length.

If a plant character that increases seedling advantage in open post-fire sites also increases flammability, then the rapid invasion of flammability is easy to explain as a positive feedback niche-construction effect (Bond and Midgley 1995, Kerr et al. 1999). Selection for a trait that affects only the probability of crown fire and fire spread (such as lower dead branch retention) may be possible where selection sufficiently favors serotiny (Kerr et al. 1999, Schwilk unpubl.). Should serotinous individuals need hotter temperatures or increased probability of complete crown fire to open seed cones, selection may favor increased flammability. Flammability in association with fire-cued germination traits is likely to create strong selective feedback mediated through the environment.

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Appendix I: Ecological and phylogenetic data sources

Thirty-eight pine species for which we had both ecological and phylogenetic data. Ecological data sources: (a) Keeley and Zedler 1998, (b) Kozlowski 1973, (c) McCune 1988, (d) Schwilk and Ackerly unpubl. Phylogeny sources: (1) Adams and Jackson (1997), (2) Bergmann and Gillet (1997), (3) Conkle et al. (1988), (4) Govindaraju et al. (1992), (5) Karalamangala and Nickrent (1989), (6) Kaundun et al. (1997), (7) Krupkin et al. (1996), (8) Liston et al. (1999), (9) Malusa (1992), (10) Millar et al. (1988), (11) Strauss and Doerkson (1990), (12) Wang and Szmidi (1993), (13) Wang et al. (1999), (14) Wheeler et al. (1983).

Specific epithet	Ecological data sources	Phylogeny sources
<i>albicaulis</i>	a, c, d	8, 11
<i>aristata</i>	a, c, d	2, 4, 8, 9, 13
<i>attenuata</i>	a, c, d	2, 4, 8, 10
<i>balfouriana</i>	a, c, d	9, 13
<i>banksiana</i>	a, c, d	2, 4, 13
<i>brutia</i>	a, d	3, 6, 7, 13
<i>cembra</i>	a, d	2, 4, 8, 13
<i>cembroides</i>	a, c, d	8, 9
<i>clausa</i> (var. <i>clausa</i>)	a, c, d	1, 2, 14
<i>contorta</i> (var. <i>latifolia</i>)	a, c, d	2, 4, 7, 8, 11, 14
<i>coulteri</i>	b, c, d	4, 7, 8, 11
<i>echinata</i>	a, c, d	1, 4, 8
<i>edulis</i>	a, c, d	2, 4, 9, 11
<i>elliottii</i> var. <i>densa</i>	a, c, d	1, 4
<i>engelmannii</i>	a, d	5
<i>halepensis</i>	a, d	3, 6, 8, 13
<i>jeffreyi</i>	a, c, d	2, 4, 7
<i>lambertiana</i>	a, c, d	4, 8, 11
<i>leophylla</i>	a, c, d	4, 5, 7, 8, 11

<i>merkusii</i>	a, d	8, 12, 13
<i>monophylla</i>	a, c, d	9, 11
<i>muricata</i>	a, c, d	2, 4, 10
<i>palustris</i>	a, c, d	1
<i>pinaster</i>	a, d	8, 13
<i>ponderosa</i>	a, c, d	2, 4, 5, 7, 8, 11
<i>pungens</i>	a, c, d	1
<i>quadrifolia</i>	a, c, d	9
<i>radiata</i>	a, c, d	2, 4, 7, 10, 11
<i>resinosa</i>	a, c, d	4, 7, 8
<i>rigida</i>	a, c, d	1, 2, 4
<i>sabiniana</i>	c, d, d	4
<i>serotina</i>	a, c, d	1
<i>sibirica</i>	a, d	2, 12
<i>strobilus</i>	a, c, d	2, 4, 8, 13
<i>sylvestris</i>	a, d	2, 4, 7, 8, 12, 13
<i>taeda</i>	a, c, d	1, 2, 4, 7, 11
<i>torreyana</i>	b, c, d	7
<i>virginiana</i>	a, c, d	1, 2, 7, 8, 14
