

# Dynamic Ecology

Multa novit vulpes

## Can the phylogenetic community ecology bandwagon be stopped or steered? A case study of contrarian ecology

Posted on **October 9, 2012** by **Jeremy Fox**

Phylogenetic community ecology is one of the biggest [bandwagons in ecology](#) right now (and before you get upset with me for saying that, click the link to find out what I mean by “bandwagon”). Much of this interest was sparked by [Webb et al. \(2002\)](#), who suggested that, by mapping co-occurring species onto a phylogeny of the species pool (the set of species thought to potentially be able to occupy the study site), “a simple logical framework can then be employed to infer mechanisms of contemporary coexistence” (Webb et al. 2002, p. 478). Specifically, they suggested that co-occurrence of phenotypically-similar species indicates “habitat filtering”, meaning roughly that community membership reflects species’ abilities to tolerate the local abiotic environment. Conversely, co-occurrence of phenotypically-different species means that similar species are being competitively excluded (=limiting similarity). If, as is often the case, phenotypic traits are phylogenetically conserved, so that closely-related species tend to be phenotypically similar, co-occurrence of closely-related species (“phylogenetic clustering” or “attraction”) implies habitat filtering, while co-occurrence of distantly-related species (“phylogenetic repulsion” or “overdispersion”) implies competitive exclusion. This is a simple, novel, creative, and relatively easy-to-implement idea, and so it’s no surprise that it took off. Spurred by the increasing ease of building phylogenies, dozens of studies have now applied this “simple logical framework” to make inferences about coexistence mechanisms without the need for difficult and time-consuming experiments.

The problem is, this “simple logical framework” is wrong.\* In fact, [there are many reasons why phenotypically-similar species might coexist besides “habitat filtering”](#). Further, the idea of “limiting similarity”, which Webb et al. take for granted, is a zombie idea; it’s long since outdated. Modern coexistence theory tells us that competing species must always be both sufficiently similar in relevant respects, as well as sufficiently different in other relevant respects, in order to stably coexist. Specifically, species need to be sufficiently similar in what might be termed “overall competitive ability”: if species are different in the sense that one is *inferior* to the other, that difference promotes exclusion, not coexistence. Species need to be sufficiently different in ways that weaken interspecific competition relative to intraspecific competition, thereby conferring a relative fitness advantage on rare species (which by definition experience mostly interspecific competition) and allowing those species to “bounce back” rather than go extinct. For all these reasons and others, there’s no clear theoretical expectation about whether co-occurring species will be more or less phenotypically similar than expected by chance, and so no way to reliably infer contemporary coexistence mechanisms simply by mapping co-occurring species onto a phylogeny, no matter whether phenotypic traits are phylogenetically conserved or not. And so we probably shouldn’t be surprised that empirical studies find mixed results: phylogenetic clustering is most common, but overdispersion and randomness are not uncommon, and the determinants of clustering vs. overdispersion remain unclear ([Vamosi et al. 2009](#)). Other lines of empirical evidence, such as competition experiments among species of varying relatedness, also provide mixed results (e.g., [Cahill et al. 2008](#)). Obviously, there could be all sorts of reasons for these mixed results, but they don’t necessarily need any special explanation at all. Mixed empirical results are precisely what you expect if your hypothesis is unfounded in the first place.

None of the points in the previous paragraph are original to me. They’re made much better than I just made them by [Mayfield and Levine \(2010](#); hereafter M&L). Many papers (including, to their credit, Webb et al. themselves) discuss modifications, elaborations, exceptions, and qualifications to the core ideas of Webb et al. But M&L is, as far as I know, the first paper to argue that the core idea of Webb et al. is fundamentally flawed.

Which provides an opportunity for an interesting case study: What happens when you [push back against a bandwagon](#)? How do other researchers react? Do early reactions to the pushback provide any hints as to whether the bandwagon will eventually stop or be redirected, or whether it will continue on as if the pushback had never happened?

For reasons I’ve discussed before, bandwagons in science are difficult to stop or steer. But M&L have a number of factors working in their favor. They published in the highest-impact ecology journal in the world, Ecology Letters. No one has any excuse for failing to notice their critique. They’re both established researchers, and Jon Levine in particular is quite prominent, so people should read what they have to say and take it seriously. Their paper doesn’t use any math which might scare off some readers. And their paper has a positive as well as a negative element. They suggest that it would be very valuable to link modern coexistence theory to patterns of phylogenetic relatedness (although they suggest no simple recipe for doing this, because none exists). People are more likely to drop their current approach if you suggest an alternative.

Even if you don’t agree with M&L’s critique, I hope you’ll agree that this is an interesting case study of a [contrarian](#) attempt to stop or steer an ongoing bandwagon. You have a situation where lots of people are pursuing a particular question using a particular approach. But then someone well-known publishes a serious, easy-to-understand critique of that approach in a very prominent venue, and suggests an alternative approach. What happens next?

To find out, the first thing I did was to look up how often M&L have been cited. Has their critique in fact been widely noted, as you'd expect? As a baseline, I looked up how often Webb et al. 2002 (the paper that more or less founded this area of research) and Vamosi et al. 2009 (a recent major review of this area of research) have been cited since M&L was published. If lots of people are citing Webb et al. and Vamosi et al., but not citing M&L, that's a sign that their critique isn't being widely noted.

M&L was published in the September 2010 issue of Ecology Letters and has been cited 38 times since, according to Web of Science. In contrast, Webb et al. has been cited 211 times since Sept. 1, 2010. Now, Webb et al. discuss other ideas about phylogenetic community structure besides the idea critiqued by M&L, and so many of the citations of Webb et al. likely are for reasons independent of the M&L critique. But still, the order-of-magnitude difference here is striking. Vamosi et al. is a review of precisely the same topic critiqued by M&L, and so one might expect that most papers that have reason to cite Vamosi et al. would have equal reason to cite M&L. But Vamosi et al. has been cited 76 times since Sept. 1, 2010, twice as often as M&L. Of course, Vamosi et al. was published the year before M&L, and so some studies citing Vamosi et al. but not M&L likely were already in review or in press before M&L was published. But even if we restrict attention to papers published since Sept. 2011 (a year after M&L was published), we find that Vamosi et al. has been cited 41 times, and M&L only 27 times. So while M&L has hardly gone unnoticed, many papers which you'd think would have good reason to cite M&L don't do so. Now, it's possible some papers cite Vamosi et al. but not M&L for good reason; you'd need to read those papers in detail to find out. But it sure seems like there might well be some papers out there proceeding as if M&L had never been written. Which is a rather depressing possibility.\*\*

But it's not as if M&L have been ignored entirely; they've been cited 38 times in two years. Of course, not all citations are created equal; papers are cited for all kinds of reasons. So I skimmed each of the 38 papers citing M&L (in one case only looking at the abstract, as the full text wasn't available to me) and classified them into categories based on how they cited M&L. In most cases, a paper fell into only one category, but in a couple of cases M&L were cited in different ways in different parts of the paper, so I included the paper in multiple categories. Applying this classification system obviously involved judgement calls on my part. But because I only used a small number of broadly-defined categories, there were only two ambiguous cases. And every paper fit somewhere in my classification scheme, except for one that I ignored because it was in Spanish and I can't read Spanish. Here are the categories:

1. Papers that aren't about inferring coexistence mechanisms from phylogenies. These papers cite M&L for various reasons, often for their review of modern coexistence theory and critiques of "limiting similarity".
2. Papers that are about inferring coexistence mechanisms from phylogenies, that cite M&L only in passing. These are papers that cite M&L, but not so as you'd notice; they proceed more or less as if M&L had never been written. Some cite M&L by first citing Webb et al. and a bunch of other papers and then writing "but see M&L". Others cite M&L in such a way that you wouldn't know from the citation that M&L was a fundamental critique of the ideas of Webb et al.
3. Papers that are about inferring coexistence mechanisms from phylogenies, that cite M&L as one paper among many. These papers typically lump M&L in with other papers discussing elaborations, modifications, qualifications, or exceptions to the ideas of Webb et al.
4. Papers that are about inferring coexistence mechanisms from phylogenies, that specifically discuss M&L briefly.
5. Papers that are about inferring coexistence mechanisms from phylogenies, that discuss M&L at length. This category includes papers based on the ideas in M&L.
6. Papers that miscite M&L, for instance by citing them in support of claims that they themselves actually deny. I was conservative in deciding whether to classify papers into this category. Merely citing M&L in passing or in a vague way (e.g., as part of a long list of papers cited in support of some broad claim) wasn't enough for me to list a paper here, even though such citations could leave an unknowing reader with a mistaken or vague impression of the content of M&L.

If M&L is having an impact on phylogenetic community ecology, you'd expect citations of it to mostly fall into categories 4 and 5. Papers in category 1 aren't directly relevant for purposes of this post, but they're indirectly relevant in a couple of ways. On the one hand, any recognition of the arguments of M&L, even in a paper that's not about inferring coexistence mechanisms from phylogenies, presumably helps to increase awareness of M&L. On the other hand, insofar as papers citing M&L fall into this category, it means papers that *are* about inferring coexistence mechanisms from phylogenies *aren't* citing M&L. Citations in category 2 suggest a bandwagon that's rolling along more or less unstopably. If most citations of M&L are in category 2, it suggests M&L will have roughly the same effect on phylogenetic community ecology as Clarence Darrow's closing speech had on the outcome of the Scopes trial--i.e. little or none (H.L. Mencken wrote that ["The net effect of Clarence Darrow's great speech yesterday seems to be precisely the same as if he had bawled it up a rainspout in the interior of Afghanistan."](#)) Citations in category 3 don't suggest lack of impact, exactly, although they do indicate that the authors don't see M&L as distinct from papers suggesting modifications, elaborations, or caveats to Webb et al. (personally, I do see M&L as quite distinct, but I suppose the point is arguable). And whether or not M&L are having any impact, there shouldn't be any citations in category 6. There's no good excuse for miscitations.

Here are the numbers. In some cases, ranges are given because of a couple of ambiguous cases:

- 1 (papers on other topics): 18-19 papers
- 2 (cited in passing): 8-9 papers
- 3 (cited as one paper among many): 4-5 papers
- 4 (discussed briefly): 6 papers

5 (discussed at length): 3 papers

6 (miscited): 2-3 papers

These results surprised me. I expected that M&L would mostly have been cited in passing or as one paper among many—that it would be widely noted, but only in a relatively cursory way. But roughly half of all citations of M&L are by papers that aren't even about inferring coexistence mechanisms from phylogenies at all. M&L is most often cited simply as a review of modern coexistence theory or as a critique of the idea of limiting similarity. In a way I think that's good; anything that helps modern coexistence theory penetrate the collective consciousness of ecologists is good. But on the other hand, it means that papers about inferring coexistence mechanisms from phylogenies have only cited M&L about 18 times since it was published, compared to many more citations for papers developing or reviewing the ideas that M&L critique. That doesn't seem to me like a bandwagon that's going to be stopped or steered by M&L. It's much like the pattern you see with the intermediate disturbance hypothesis, where the papers that originally developed the idea continue to be cited *far* more often than papers critiquing the idea.

As for the remaining categories, it's unsurprising but a bit depressing to see category 2 (citations in passing) as the largest remaining category, comprising almost half of the remaining papers. On the other hand, I'm pleasantly surprised to see that papers that specifically discuss M&L (whether briefly or at length) collectively outnumber those which just lump M&L in with the many other papers that have discussed elaborations or modifications of the ideas of Webb et al. I had thought category 3 would be a big one but it's not.

Probably the biggest cause for hope for an M&L fan like me are the three papers in category 5. [Kuntsler et al.](#), [Hultgren and Duffy](#), and [Anderson et al.](#) are all based largely on the ideas of M&L. These authors are the first to take up the positive suggestions of M&L. I could see these papers having an impact. Often, the most effective way to critique an established approach is not to criticize it directly, but simply to do things differently, and show that doing things differently leads to novel insights that wouldn't have been discovered under the established approach. I note with interest that all three were published in very high-profile journals (two in Ecology Letters, the other in Journal of Ecology). [Usinowicz et al.](#) in the latest issue of Ecology is another terrific example of a paper taking a different approach to link coexistence mechanisms and phylogenies (although phylogenetics isn't the main focus of the paper, so it actually doesn't cite M&L even though it's thoroughly grounded in modern coexistence theory). Perhaps the phylogenetic community ecology bandwagon will start to change course as more ecologists begin to realize that following the lead of M&L is a good way to get a high-profile publication.

Our papers sometimes have their greatest impact in ways the authors never expected. My former labmate Jill McGrady-Steed did one of the first experimental tests of biodiversity-ecosystem function relationships (McGrady-Steed et al. 1997 Nature). At the end of the experiment, just for the heck of it, she tried invading all her communities with a species not used in the experiment, and found that the invader only invaded species-poor communities. That throwaway result on the diversity-invasibility relationship turned out to be the main thing people cited her for. Maybe M&L, and those who follow their lead, won't end up having much impact on the phylogenetic community ecology bandwagon, but will end up having a big impact by helping to spread the word about modern coexistence theory. Which might prevent some future unfounded idea about how to infer coexistence mechanisms from ever being proposed in the first place.

Of course, there's also the question of the impact this blog post will have. 😊

\*As always, in saying that Webb et al.'s idea is wrong, I imply no personal criticism of any of the authors. They're all very smart and very good ecologists, and Mark McPeck in particular is a friend. But everyone makes mistakes, including serious ones.

\*\*I am of course unable to quantify the number of papers that M&L prevented from being written or published. That is, perhaps some ecologists who might otherwise have written papers based on Webb et al. changed their plans after reading M&L, or perhaps they had their papers rejected by referees and editors convinced by the critique of M&L. But if I had to guess, I'd bet that the number of such papers is at most very small.

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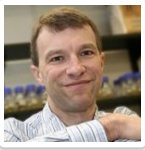
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About Jeremy Fox

I'm an ecologist at the University of Calgary. I study population and community dynamics, using mathematical models and experiments.

[View all posts by Jeremy Fox →](#)



**Brian J. Enquist**

on **October 9, 2012 at 6:13 am** said:

Jeremey, I appreciate your comments but I worry that your post is overly polarizing, does not offer an alternative way forward, and does not give credit where credit is due. I also don't agree with your conclusion that Webb et al. 2002 is "wrong". I have always seen phylogenetic approaches to community ecology as brining in another important tool to help document pattern – especially when a regular species list cannot reveal much detail of structure. Why criticize an important tool kit that helps us further document pattern and differentiate hypotheses? Like you, I also appreciated the M&L contribution (see also Cavender-Bares et al. 2008 EcoLets paper (Table 1) for a similar set of conclusions). Sure, we can debate what causes clustered or overdispersion but I would think you would agree that having another metric to help us differentiate potential processes is an important breakthrough. Webb et al. 2002 offered a novel set of methodologies to quantify additional information about the structure of community diversity. I agree we should be skeptical of bandwagons – and blindly using methods without questioning results – but let's give credit where credit is due. A species list to calculate richness and species:genus ratios can only go so far.



**Jeremy Fox**

on **October 9, 2012 at 2:06 pm** said:

Hi Brian,

Thanks for your comments.

Just so you know, before posting I ran this post by a colleague who works on this topic. My colleague liked it very much. I get that you don't agree with what I said, which is fine—I certainly don't expect universal agreement with this post! ~~But with respect, I don't see what's "unfair" about the post. Can you elaborate? Do you think M&L are "unfair" too? Do you think it's unfair to expect people working in this area to cite M&L, and not to cite M&L merely in passing?~~ CORRECTION: Not sure why I wrote that bit about unfairness, that's not a word you actually used. It was early in the morning when I replied to your comment, but that's an explanation, not an excuse. My bad. FWIW, I am still curious about your views on M&L, since all I tried to do in my post was call attention to their work and look at how it's been cited. If you think my post is unduly critical or polarizing, or doesn't give credit where it's due, do you think the same of M&L?

Re: the post being "polarizing", I would suggest that the post merely articulates latent polarization in the field. I received very positive feedback on the post this morning from another colleague who works on this topic, who once got into an argument with his collaborators who wanted to completely ignore M&L. I don't this post creates controversy where none would otherwise exist. I think this post articulates what a lot of very smart community ecologists who don't work primarily on phylogenetics think of phylogenetic community ecology.

Re: my not offering a way forward, I'm afraid I don't understand why you say that. I cited four papers that I think exemplify the way forward. Ulanowicz et al. in particular looks very cool (I've only had time to skim it as yet). It's true I haven't offered an \*easy\* way forward, a simple "cookbook recipe" that people can follow in order to infer contemporary coexistence mechanisms from easy-to collect observational data. That's because no such recipe exists. No one said ecology was easy.

Re: Webb et al. 2002 being "wrong", I think my post makes very clear which specific claims of Webb et al. that I think are wrong, and the reasons why I think they're wrong. Nowhere in the post did I claim that everything Webb et al. said in their entire paper was wrong. My reasons for thinking those specific claims of Webb et al.'s are wrong are the same as Mayfield and Levine's. I stand by my statements on this.

Re: phylogenetic methods being more informative than looking at species-genus ratios, that seems to me to be damning phylogenetic methods with faint praise. Further, your comment seems to imply that looking at species-genus ratios is the only other way to do the things that people are trying to do with phylogenetic methods. With respect, I strongly disagree. There are \*lots\* of other ways to infer contemporary coexistence mechanisms besides looking at species-genus ratios. We can, for instance, ex-

perimentally test hypothesized coexistence mechanisms. We can, as in the work of Jon Levine and colleagues, parameterize dynamical models of communities and use those models to simulate experiments that would be physically impossible to conduct, in order to infer the strength of hypothesized coexistence mechanisms. Etc.

You seem to feel that phylogenetic methods provide an important descriptive advance—that it's important or useful to have this description in order for us to make progress, perhaps because we first need the descriptive data before we can develop explanations for it. I don't disagree with that broad point. There are many cases in science where advances in conceptual or mechanistic understanding have followed advances in descriptive understanding. But in this particular case, I don't know that I agree. I don't think community ecology was crying out for new descriptions of community structure, to give theoreticians new targets to shoot at. We already have a bazillion ways to describe community structure. In particular, if you want to make inferences about mechanisms of contemporary coexistence (which, as the quoted sentence indicates, is what Webb et al. wanted), well, what's preventing us from making those inferences for most systems is *\*not\** lack of descriptive data. It's lack of the right sort of experimental data. I note that Mark McPeck himself, one of the co-authors of Webb et al., has recently been emphasizing very strongly that ecologists don't routinely conduct the sorts of experiments they need to conduct to quantify the strength of different classes of coexistence mechanism (say, spatial vs. non-spatial mechanisms, or fluctuation-dependent vs. fluctuation-independent mechanisms, or stabilizing vs. equalizing mechanisms).



**Eric Larson**

on **October 9, 2012 at 2:04 pm** said:

Part of your question (is contrarian science cited as frequently as what it's contradicting? is it cited correctly?) relates to a recent paper in Ecosphere: "Do rebuttals affect future science?"

<http://www.esajournals.org/doi/pdf/10.1890/ES10-00142.1>



**Jeremy Fox**

on **October 9, 2012 at 2:08 pm** said:

Wow, thanks Eric, I hadn't seen that yet. That looks like a really interesting paper, *\*very\** bloggable! Will have to do a post on it ASAP.



**Michael E. Smith**

on **October 9, 2012 at 3:44 pm** said:

I am an archaeologist, and bandwagons are rampant in my field (archaeological study of states and empires). I have usually attributed this sorry state of affairs to the heavy doses of humanities thinking (including postmodernism) among archaeologists. I sometimes look to fields like ecology as paragons of scientific rigor in comparison to the low scientific standards in my field. So it is illuminating (and depressing) to find bandwagons and studied non-citation of strong critiques, in ecology. Nice post.



**Jeremy Fox**

on **October 9, 2012 at 4:33 pm** said:

Glad you liked the post Michael.

As I said in my old post on bandwagons in ecology, I do think bandwagons in ecology typically get started for good scientific reasons. They're not *purely* fads like a trend towards skinny jeans or whatever. There certainly are examples of good papers using phylogenetic information to inform our understanding of current ecological communities. But I think these days, such good papers on phylogenetic community ecology are outnumbered by lower-quality papers. And I do think that "momentum" inhibits the field from collectively stepping back and rethinking the entire approach.

To be clear, while I certainly am disappointed in the number of papers citing M&L only in passing or not at all, I wouldn't necessarily call those "studied" non-citations. I have no idea if any of the authors who failed to cite M&L, or who cited M&L only in passing, thought to themselves "Let's not cite M&L, so as to avoid undermining our own paper, and hope the referees don't call us on it." If I had to guess, I'd say such studied, cynical behavior is rare at most in ecology (I certainly hope it is!) So while I do think there are numerous papers that should've cited or discussed M&L but didn't, I can imagine lots of less-cynical and non-cynical reasons for this (including subconscious reasons).



**Michael E. Smith**  
on **October 9, 2012 at 4:41 pm** said:

Unfortunately, this kind of "studied, cynical behavior" is all too common in my own field. I recently read a work on confirmation bias, and my first thought was that the author must be talking about my field!:

"There is an obvious difference between impartially evaluating evidence in order to come to an unbiased conclusion and building a case to justify a conclusion already drawn ... It refers usually to unwitting selectivity in the acquisition and use of evidence. The line between deliberate selectivity in the use of evidence and unwitting molding of facts to fit hypotheses or beliefs is a difficult one to draw in practice." (pp. 179-180)

Nickerson, Raymond S., 1998, Confirmation Bias: A Ubiquitous Phenomenon in Many Guises. Review of General Psychology 2 (2): 175-220.

(17-180).



Jeremy Fox  
on **October 9, 2012 at 4:46 pm** said:

That quoted passage is a wonderful summary of confirmation bias. I think it's one of the most important obstacles to doing good ecology, and also one of the hardest to overcome. I certainly wouldn't claim I'm immune to it.

I sometimes think that our best hope in science is that others have *\*different\** confirmation biases than we do, so will help to keep us honest.

Duncan Watts' Everything is Obvious (Once You Know the Answer) is one good popular treatment of confirmation bias and other cognitive biases. I'm sure there are others with which I'm not familiar.





**Jeremy Fox**

on **October 9, 2012 at 9:05 pm** said:

Worth noting that none other than Jon Losos himself recently pushed back against the phylogenetic community ecology bandwagon in his American Society of Naturalists Address: <http://www.jstor.org/stable/info/10.1086/660020>

Losos is more famous than Mayfield or Levine, and he's used phylogenies a lot in his own work. Both reasons why his attack might have more bite. But his attack is also more broadly-directed (hence it's probably easier for any individual to think "he's not directing this at me"), and like M&L he doesn't offer any \*easy\* way forward. Both reasons why his attack might fall largely on deaf ears.

As I think I've noted in other posts, David Ackerly gave a great talk at the ESA meeting back in 2009 or so making many of the points made in this post and more. He too is a really famous phylogenetic/trait-based ecology guy, so you'd think his attack might have some bite. But sadly, he never got around to turning the talk into a paper, and having talked to him I have the impression he's moved on to other things. So only people who saw the talk will have been impacted. I tried to get him to at least put his slides online with the idea that I'd do a blog post plugging them, but he didn't bite.



**darmitag**

on **October 9, 2012 at 11:29 pm** said:

Besides the conceptual issues addressed here, there are a number of methodological problems that are rarely addressed in these types of analyses stemming from 1) completely incorrect statistical significance testing, 2) lack of justification of an appropriate 'regional taxa pool', and 3) unjustified use of a particular null model without consideration of alternatives. The first issue is easily addressed, but the second and third are more problematic, and can really affect the interpretation of results. One thing worth considering, based on your list of alternatives to habitat filtering, is that these phenomena are not mutually exclusive and our measuring their relative strengths depends on the phylogenetic scale at which experiments are designed/matrices are randomized/etc. Time and experiments will ultimately prove the utility of such an approach. That Losos paper nails it with the statement "Much more frequently, phylogeny will serve as a great tool to generate hypotheses about process but not to test them directly." That said, I think ecology requires a more meaningful way to describe biodiversity, and phylogenetics is a step in the right direction.



**Jeremy Fox**

on **October 10, 2012 at 12:39 am** said:

Certainly, the second issue at least is widely recognized. If memory serves, Webb et al. raise it, and there are studies that try to get at it (and the related issue of the spatial and phylogenetic scale at which the local community is defined) by varying the definition of "local" and "regional" and seeing how it affects the results.

I intentionally avoided these other issues not because they're unimportant, but because at least some of them have been widely discussed (in contrast to the critique of M&L), and because they seem to me to be less fundamental. The M&L critique still applies even in a hypothetical "best case scenario" where all the technical issues you identify have been satisfactorily addressed.

Personally, when I think of studies that make compelling use of phylogenetic information as part of a story about the historical and current evolutionary community ecology of some group of organisms, I think of long-term research programs that have integrated phylogenetic information with a massive range of other experimental, observational, and comparative data in a rich way (as opposed to a "follow this simple recipe" way) to address all aspects of a nest of interrelated questions. I'm thinking of things like the decades of work of the Grants and their students on Darwin's finches, the work of Losos and many others on Caribbean anoles, and the work of Schluter, MacPhail, and colleagues on threespine stickleback in postglacial BC lakes. Notably, those are research programs where there's "two-way information flow" between phylogenetics and

studies of contemporary communities. Our knowledge of the current community, gained via experiments and other means, informs our interpretation of the phylogenetic history, not just vice-versa.

As to whether phylogenetics is a descriptive advance towards “meaningful” descriptions of biodiversity, it certainly could be in some cases. Whether it's meaningful, and more meaningful than non-phylogenetic descriptions, depends on the question one is asking. For the most part, I don't tend to see lack of appropriate ways of describing or summarizing community structure as the “rate limiting step” in improving our understanding of current community ecology. But I suppose the point is debatable.



Nathan Kraft  
on **October 10, 2012 at 4:06 pm** said:

Hi Jeremy- My understanding is that many people who work in this area do take the M&L paper to be pretty serious challenge to the original framework that Webb et al laid out, but this is not the first challenge to the framework out there- Cavender-Bares et al. 2009 for example really did a very helpful job laying out the challenges in linking pattern to process in these types of analyses (see their table 1). M&L have added another very important item to the list, so in that respect it may not be the first thing people think of (or cite) when they consider complications to the original Webb et al. 2002 paper. In short, there are many processes that can generate similar phylogenetic patterns. In regards to your double asterisk point at the end of the post, my sense is that the M&L paper has prevented more papers then you might think from making it through review- I think it is ratcheting up the bar for contributions in this area. I agree with your sentiment that going forward there is likely a limited role for simple null model analysis of phylogenetic structure in the absence of other information (functional traits, experiments, demographic modeling, etc) in all but the most challenging of systems to study, but I think things have been trending this way for a while now...



**Jeremy Fox**  
on **October 10, 2012 at 6:11 pm** said:

Thanks for your comments Nathan, it's good to hear from people who actually work on this stuff.

Your comments jive with those I've heard in private correspondence from others who work on this stuff—that the best people, at least, have moved on from the simple Webb et al. framework, under the influence not just of M&L but of other papers, in particular Cavender-Bares et al. I think that trend is a good thing. Cavender-Bares et al. certainly don't try to offer any simple “recipes” for how to proceed, for which thank goodness. I guess I still do question whether things are changing as fast as they should. Papers have still been published in good journals in the past couple of years based more or less on the ideas of Webb et al. But perhaps that's just me being overly impatient with the pace of change in the field. I tend to feel that the “simple logical framework” of Webb et al. 2002 should never have gotten off the ground in the first place (the critique of M&L would've been just as valid in 2002 as in 2010), much less still be even semi-viable a decade later.

You suggest that M&L have added one more important item to the list of challenges identified by Cavender-Bares et al. You don't think M&L is a rather more fundamental critique than that? I agree that Cavender-Bares et al. absolutely have a lot of useful things to say. But to my mind, their discussions of how species interactions affect coexistence are still structured around an outdated, non-Chessonian view of how coexistence works. Cavender-Bares frame their discussion of coexistence in terms of reasons why competition among close relatives might be “strong” or “weak”. From the point of view of modern coexistence theory, that way of framing things is crucially ambiguous. Species coexist when they can increase on average when rare. Species can coexist when interspecific competition is “strong”, and fail to coexist when interspecific competition is “weak”, depending on how strong intraspecific competition is. If you want to figure out how to use phylogenetic information to inform understanding of coexistence, surely your starting point has to be the best-developed general theory of how coexistence works? With issues trait conservation and phylogenetic scale and spatial scale and etc., important as they undoubtedly are, being secondary?





Nathan Kraft  
on **October 15, 2012 at 7:49 pm** said:

I think the M&L paper is the first one that I was aware of that explicitly challenged the “competition” predictions of the Webb et al paper, and in that sense it was a step up from earlier papers that added more detail the that 2002 set of predictions. I think any efforts to bring a more modern, “Chessonian” view of species interactions into these types of analyses is a very very good thing for everyone involved. But I also think there are clearly some gaps out there that I haven't seen good answers for yet. Both Webb 2002 and M&L (via Chesson) are built around the same phenomenon of a push-pull effect on phenotypes within a community- for Webb this is competition vs. habitat filtering, for M&L this is niche vs. fitness differences. For what it's worth, I don't know of a good mapping of the concept of “habitat filtering”- which has a long history in plant ecology in particular- to the Chessonian view of species interactions. How different is “habitat filtering” from “fitness differences”, for example? I agree that the framework needs to be updated for sure, but I'm not sure that all the pieces are there yet to build the correspondences between them. If anyone knows of a paper that does this, I'd love to see it...



**Jeremy Fox**  
on **October 15, 2012 at 8:25 pm** said:

Personally, I have no idea what “habitat filtering” is supposed to mean, really. It's one of these vague, purely verbal ideas that people seem to define however it suits them. Indeed, two of the papers that miscited M&L did so by citing them for the notion that “habitat filtering” be redefined in an extremely broad way—a possibility that M&L themselves raise *and then reject*. My own personal view is that the whole idea of “habitat filtering” takes the metaphorical idea of “filters” on local community composition far too literally, and we'd be better off if we junked it. That a concept has a long history in some field doesn't mean it deserves to be retained. The notion of “limiting similarity” has a long history—and it's a zombie idea. The intermediate disturbance hypothesis has a long history—and it's a zombie idea.

Re: Chesson's ideas also being built on a “push-pull” effect on phenotypes, I don't think that's correct, at least not necessarily. How phenotypic traits map onto the strength of niche differences and fitness differences is very case-specific, and depends on biological details that have nothing to do with coexistence theory per se. For instance, in theoretical models, tweaking a single model parameter often will alter the strength of both niche differences and fitness differences, sometimes in the same way, sometimes in opposing ways. And that's even before we start worrying about how model parameters might or might not map onto the underlying morphological and physiological phenotypic traits that investigators typically measure. I'd like to see people studying (theoretically, and empirically) the mapping from phenotypic traits to coexistence mechanisms, rather than starting from *assumptions* about how the two are linked and then making inferences based on those assumptions. Going in the direction I'm suggesting will of course require people to start quantifying coexistence mechanisms directly, rather than trying to infer them from trait data or phylogenetic data. Folks like Amy Angert are starting to go in this direction. It's not easy. Rigorous work never is.

Personally, I don't know that I'd suggest trying to identify correspondences between ideas like those of Webb et al. and Chessonian ideas. By all means, let's think about how one might expect the strength of equalizing and stabilizing mechanisms to evolve, and how equalizing and stabilizing mechanisms arise from the phenotypic traits of the interacting species. But let's not do that by first trying to “translate” Chessonian ideas into a language that doesn't fit them, or conversely try to “translate” non-Chessonian ideas into Chessonian language. That would simply lead to confusion, and to taking as our starting point a distorted, mistranslated view of how coexistence works. Instead, let's just admit that Webb et al. started down a blind alley, conceptually, and that our only choice is to go back to square one and start over.



Trevor Branch

on **October 11, 2012 at 5:40 am** said:

I was fascinated to hear about this discussion in a field different to my own, fisheries, where bandwagons are a way of life. I'm a coauthor on the paper mentioned in the comments: Banobi, J. A., T. A. Branch, and R. Hilborn. 2011. Do rebuttals affect future science? Ecosphere 2(3):art37. doi:10.1890/ES10-00142.1. What we found was essentially uncritical acceptance of all original papers (95% positive citations) despite multiple rebuttals to each.

I recently also looked at one paper that made a prediction about complete fisheries collapse by 2048, with 10 rebuttals, and found that the original authors have only referred to their own 2048 prediction in 1 of 55 subsequent citations. While the original authors appear not to have faith in their own prediction, others have mentioned it in 77 papers.

Just a note about citation rates over time. You will find citations are negligible the year of publication, and then gradually rise to a peak 3-10 years after publication. So a valid comparison with citations of Mayfield and Levine (2010) published in Sept 2010 to citations of Webb et al. (2002) published August 2002, would be to compare M&L citations in 2010-2012 (38 citations) to Webb citations in 2002-04 (31 citations). By this metric the rebuttal is actually getting cited more\* than the original was. It will just take time to build up.

\*I ignore the correction needed for more papers in total being published in 2010-12 than 2002-04.



Jeremy Fox

on **October 11, 2012 at 5:43 am** said:

Thanks for your comment Trevor. You've unwittingly previewed an upcoming post! I'm embarrassed to say that I wasn't aware of Banobi et al. until another commenter on this post pointed it out to me. I went and read the paper and liked it very much. There's a post on it scheduled to go up later this week.

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Pingback: [Existing data, and easy-to-collect data, cannot answer many of our questions | Dynamic Ecology](#)



Jim Bouldin

on **October 14, 2012 at 8:12 pm** said:

Apologies for not reading the full article but I hope to come back to it. For now just throwing this only partially related question out there.

Does anyone recall, off the top of their head, any studies in which taxon coexistence has been assessed based on extremely limited plot data? By "limited" I mean very few taxa recorded at each sampling location (but at potentially many such locations). I am working on a new method for assessing tree coexistence using land surveyors' tree data from 19th century (pre-settlement) forests in different parts of the U.S, in which the sampling was such that taxa for only two to four trees was typically recorded (but in an enormous number of plot-less sampling locations). I have an analytical approach +/- worked out at at this point but have not looked in depth at the literature yet (yes that's potentially bassackwards, I realize).

Thanks in advance for any recollections, however vague.

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**Gordon G McNickle (@GGMcNickle)**

on **March 27, 2014 at 7:25 pm** said:

I know this is an old post, but I just came across it. Thanks, I've always been suspicious of the assertion that phylogenetic similarity implies functional similarity, but hadn't seen M&L. I shall keep it close.

