Explanation of residual variance is no cause for alarm

As regular members of the University of Oklahoma's ecology journal club, we read with interest Low-Décarie *et al.*'s (*Front Ecol Environ* 2014; **12[7]**: 412–18) gloomy prognosis for ecology. Like them we were alarmed, initially, to see a steep drop in explanatory power in our field, reported as a linear decline over the past several decades in R^2, the coefficient of determination, an estimate of how much variance in a response variable is accounted for by one or more predictors.

The authors offered three explanations for the decline in R^2. First, ecologists have plucked the "low-hanging fruit"; this idea proposes that readily doable studies were completed long ago, but it does not follow that more easily answered questions – those referred to as low hanging – explain a higher proportion of variance. Second, as research accumulates, we approach ecology's mean R^2, a "law of large numbers" argument in which we have a progressively better estimate of the true mean. It is unlikely that the estimate of any mean would decrease monotonically with greater accuracy; that is, the standard error (SE) around our estimate of 0 will shrink, but the expected value of 0 is no more likely to increase or decrease as SE shrinks. Third, systemic bias has affected *Ecology*, the *Journal of Ecology*, and the *Journal of Animal Ecology* (the journals from which Low-Décarie and colleagues culled data), an idea that requires all three journals to have become biased in a parallel manner as their impact factors changed.

Each explanation could lead to anxiety about the future of ecological research, and anxious is precisely the tone conveyed in the paper. Alternatively, we believe that a fourth explanation accounts best for the linear trend in R^2, an explanation predicated on the Kuhnian (1962) notion of what it means to conduct "normal science": the practice in which all scientists, no matter how clever, engage on a regular basis. Kuhn's (1962) "paradigm shifts" are exceedingly rare, but such shifts invariably raise R^2 markedly: for instance, the change in explanatory power when Einsteinian relativity supplanted Newtonian mechanics. "Normal science" progresses by baby steps rather than great leaps. Consider the theory of island biogeography (MacArthur and Wilson 1963), in which a mere two predictors – an island's size and distance from a mainland source (a proxy for colonization rate) – account for a large amount of variation in species richness. A recent extension of the MacArthur–Wilson model added a time component (Whittaker *et al.* 2008) as a means to incorporate the process of speciation, and found that R^2 increased. Time contributed a relatively small amount to explanatory power beyond that of the original model, yet this new model is an important advance because it provides clearer insight into factors that govern species richness on islands.

Our explanation of the pattern of declining R^2 ought to assuage ecologists' anxiety. The entire process of "normal science" is to explain residual variation, and so most researchers, without stating it explicitly, report only the novel portion of variation they explained rather than the total amount of variation that now can be explained. This goal is aided by commonly used procedures such as the partial Mantel test, which accounts for a known explanatory variable (eg geography) before it outputs an R^2 value, which by its nature is partial. Such partial values account implicitly for what we know already and for variance explained by a new variable. It is the latter – the discovery of new explanatory relationships – that drives ecological research and the reporting of it. As a consequence of this practice, it is self-evident that reported R^2 will decrease over time, even as overall explanatory power accumulates.

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The authors' reply

In "Rising complexity and falling explanatory power in ecology", we reported on a set of observations: a fall in yearly average R^2 values and a rise in the number of P values per article and per author in ecology. We then attempted to provide some working hypotheses to explain these observations, postulating that these trends may be the hallmark of a maturing science, or may indicate biases in the dissemination of science in ecology.

Our intent was not to convey a gloomy prognosis for ecology, but to invite reflection on the trajectory of our discipline. We thus applaud the engagement of this reflection by Patten and Hartnett and welcome this opportunity to further discuss our findings and proposed hypotheses. We are pleased to hear hypotheses proposed by others to explain these trends in the ecological sciences and are particularly interested in suggestions of novel empirical approaches for distinguishing between potential mechanisms.

Patten and Hartnett's hypothesis proposes that ecology is staying the course of "normal science" to expand efforts to explain residual variation, in sharp contrast to a science undergoing a "paradigm shift". We believe that this is a different, and possibly more appealing, wording of our first hypothesis. In our first hypothesis, exemplified by the metaphor of the "low-hanging fruit", the lion's share of our capacity to explain and predict is made possible by long-established theories. The "explanation of residual variation" described by Patten and Hartnett could have been substituted with our use of the term "marginal explanatory power". We did not, however, speculate on the advent of a "paradigm shift" in ecology or the advent of a new crop of fruit.

We do not identify as philosophers or historians of science, but we do feel the portrayal by Patten and Hartnett of "paradigm shift" in contrast to "normal science", sensu Kuhn, is not entirely adequate, even if this distinction may be highly subjective. We would suspect that paradigm shifts are accompanied by leaps in R^2 in the specific context that the advancement applies. While the discovery of relativity could undoubtedly be labeled a "paradigm shift", it is not because this theory offered a step improvement on Newton's theories. Rather, Einstein's theory provided explanatory and predictive power ($R^2 \rightarrow 1$) in a context where Newton's theory failed ($R^2 \rightarrow 0$) – the prediction and explanation of the movement of extremely large objects or movement at extreme speeds – while also providing explanation and prediction in all contexts where Newtonian physics had not been falsified. The effect of "paradigm shifts" on explanatory power or complexity is a suitable question for future metaknowledge studies.

We likely have not presented an exhaustive list of the possible mechanisms for the observed trends in R^2 and number of P values in ecology. These trends may be best explained by hypotheses that make reference to "normal science" and "paradigm shifts" as suggested by Patten and Hartnett, beyond what is included in the "low-hanging fruit" hypothesis. We would suggest that further metaknowledge studies are required to discern between proposed hypotheses and to accurately describe the state of our discipline.

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Rapidly spreading seagrass invades the Caribbean with unknown ecological consequences

The non-native seagrass *Halophila stipulacea* has spread rapidly throughout the Caribbean Sea (Willette *et al.* 2014); without additional research, the ecological ramifications of this invasion are difficult to predict. Biodiversity, connectivity of marine ecosystems, and recovery of degraded coral reefs could all be affected. The invasive seagrass, native to the Red Sea and Indian Ocean, has taken over sand bottoms and intermixed with or replaced native seagrasses, including *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* (Figure 1).

H stipulacea is an established invasive species in the Mediterranean Sea, probably introduced after the opening of the Suez Canal. Competition between *H stipulacea* and native Mediterranean seagrasses is minimal to absent due to habitat preferences; *H stipulacea* grows in deeper, bare sand habitats and over submerged dead mats of native seagrass (Sghaier *et al.* 2011). The only other known invasive seagrass species, *Zostera japonica*, has displaced a native seagrass at some locations off the coast of the Pacific Northwest (Jun Bando 2006). Experimental introduction of *Z japonica* to bare mud flats increased the density and number of animal species observed therein (Posey 1988). Sediment disturbance, such as the excavation of underwater substrate by storms, provides an advantage to both of these faster-growing invasives over their native counterparts (Jun Bando 2006; Willette and Ambrose 2012).

In the Caribbean, *H stipulacea* could stabilize previously unvegetated sand bottoms, thereby reducing erosion of nearby coastal shorelines during storm events, which are expected to become more frequent and stronger under a changing climate. Improved understanding of the potential effects of this invasive seagrass in the Caribbean requires more

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Figure 1. *The invasive seagrass* Halophila stipulacea *(bright green, short elliptic/oblong blades 3–8 cm long, with distinct mid-veins) growing intermixed with* Thalassia testudinum, Halodule wrightii, *and* Syringodium filiforme *near St John, in the US Virgin Islands.*