Explaination 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.

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.

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, 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

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.
data on herbivory rates, selective feeding, and relative nutritional values of the native and introduced species. For example, the proximity of seagrasses, mangroves, and coral reefs in the Caribbean supports high levels of fish biomass and diversity (Nagelkerken et al. 2001), which could decline if the invasive seagrass reduces the extent of native seagrasses, if native seagrasses are preferred by herbivorous fish, or if native seagrasses provide superior nutrition.

Recovery of degraded coral reefs (Jackson et al. 2014) could be either hindered or promoted indirectly by the spread of this invasive seagrass, depending on its effects on the abundance and diversity of herbivorous fish and sea urchins that, by feeding on algae, open up substrate for coral recruitment and growth. Preliminary data from experimental fish traps placed in seagrass beds dominated either by H. stipulacea or by S. filiforme showed the former had larger individual fish, fewer juvenile fish, and more fish species (Willette and Ambrose 2012). Notably, few herbivorous fish were caught in traps within either of these seagrass beds. Moreover, a significantly greater abundance of epibiotic (surface-attached) organisms – particularly members of the Crustacea, many of which serve as important prey species for fish – was associated with the invasive seagrass (Willette and Ambrose 2012). More data are needed on the role of H. stipulacea beds as nurseries and foraging areas for parrotfish, green sea turtles, sea urchins, and other herbivores.

Further research is also required to determine whether positive effects of the spread of this seagrass outweigh the negatives and what, if any, management actions should be taken. Given the rapid spread of H. stipulacea, only weekly monitoring of bays and removal of the invasive would keep it from getting a foothold. Physical removal of the seagrass after it has become established, however, would likely not be feasible due to logistic and monetary constraints.

H. stipulacea now joins a growing list of habitat-altering species, including the Indo-Pacific lionfish (Pterois volitans), invading the Caribbean. Caroline S Rogers1*, Demian Willette2, and Jeff Miller3
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