RESOLVING CONCEPTUAL CONFUSION AND QUANTIFYING CROSS-TAXA PATTERNS OF 'DENSITY DEPENDENCE' IN POPULATION ECOLOGY

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ABSTRACT

Density dependence *represents a causal relationship between the size of a population and at least one of its measureable demographic rates. It encapsulates the demographic and evolutionary role of a range of social and trophic mechanisms (e.g., cannibalism, competition, cooperation, parasitism, predation), whose effects on crowding and extinction are themselves modified by the population's abundance (**density feedback**). The concept is applied in conservation and management to assess critical matters such as harvest quotas, pest/invasion control and thresholds of extinction. I review the use of density dependence in ecology.*

*I quantify a temporal increase in the number of ecological papers examining this concept across an augmenting number of study taxa, and little consensus around the meaning of density dependence and associated concepts in a questionnaire survey among 136 ecologists (**Chapter 1**). Next, I revise the vocabulary of density dependence in a historical context, finding more than 60 terms, many of which are polysemous, synonymous, or grounded in opinionated statements; I name five unequivocal qualifiers of density feedback (compensatory, delayed compensatory, overcompensatory, depensatory/Allee effect) linked to known population phenomena (stability, cycles, chaos, decline), and dissect the semantic differences between density dependence and population regulation (**Chapter 2**).*

*Using empirical methods, I show that the strength of density feedback increases with the pace of species' life histories (**Chapter 3**), yet is only negligibly correlated with coarse climatic gradients (**Chapter 4**). These results suggest that broad life-history information can assist management and conservation actions when detailed demographic data are unavailable; and that many demographic processes might operate at spatial scales specific to populations, not species. Subsequently, I provide the first empirical cross-taxa demonstration that density effects on single fertility/survival rates (components) have weak association with feedback at the population level —a phenomenon I call 'ensemble' density feedback (**Chapter 5**). The major implication is that population processes can buffer variation in demographic rates, and management/conservation can be misled when based only on component density feedbacks.*

*In my corollary discussion (**Chapter 6**), I advocate for phenomenological models to characterise long-term population trends, argue that better integration of temporal and spatial demography could circumvent ongoing semantic conundrums, and highlight the need for a code of ecological nomenclature. Stronger emphasis on the comprehension, mathematical description and application of density feedback through ecological disciplines, from students to seasoned academics, is absolutely necessary for ecology to become one of the most influential branches of modern science, a tool of knowledge for improving societal and environmental well-being.*

STATEMENT OF ORIGINALITY

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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Salvador Herrando-Pérez

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Bibliography might be taken as a given but constitutes the very skeleton of research work. After conducting research and lecturing in developed and developing countries with limited resources, my access to the outstanding resources of the **Barr Smith Library** (connected to all University of Adelaide libraries) felt like living in a paradise of information — three mouse clicks to get a paper online from *all* key journals in my field, and an impressive collection of books spanning back the 19th and 20th centuries, including *all* the earliest, major ecological works by Elton, Fisher and the like. I congratulate the University of Adelaide for investing in such a vast and comprehensive bank of literature.

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FOREWORD

"At school he [Albert Einstein] was bored, intimidated, shy, and withdrawn…"
The science class you wish you ever had (Brody & Brody 1998)

I have bolstered my research skills through a PhD with a strong mathematical component, and the challenge has been of such magnitude that I feel compelled to reflect on how I managed to succeed.

From the time I did my undergraduate degree in Spain in the 1980s, universities have transformed into a form of business enterprise, where money is attracted not only through student recruitment, but also by benchmarking other universities, nationally and globally. In the growth of such capitalisation of education, I would like to think that one day someone will forge an indicator to measure the extent to which the delivery of education unleashes (or constraints) creativity, and this indicator become a universal beacon of education quality.

Standards come to mind. It is appalling that, since their earliest training, students are encouraged into a learning method that encourages storing information, and their academic merit is scored on how well they regurgitate that information in an exam. More than a century ago, Chamberlain (1890) made the cogent distinction between an 'acquisitive study' "…to follow by close imitation the processes of previous thinkers, or to acquire by memorising the results of their investigations"; and a 'creative study' "…to discover new truth, or to make new combinations of truth, or at least to develop an individualised aggregation of truth. The endeavour is to think for one's self, whether the thinking lies wholly in the fields of previous thought or not". The acquisitive style of education pervades primary, secondary, and tertiary education — I have seen or experienced it in Australia, Colombia, England, Mexico, Peru and Spain. Along the way, teachers and venues change, but students keep memorising theoretical content that will sooner or later fall into oblivion, with no benefit to individuals or society: a colossal waste of resources! This vicious machinery is sustained by reward and punishment in convoluted manners, denouncing the pedagogical void to inspire creative thinking. For instance, one of my primary-school teachers had boys seated in class by a 'ranking of intelligence'. So one could lose the first seat if the classmate in the second seat answered a question correctly, which the up-to-then 'most intelligent' had failed to hit. The competition to occupy the first seat and shame to sit in the last one are metaphors for our atrocious modern societies and academic institutions. How many Beethovens, Christies, Einsteins or Van Goghs

(all documented dyslexic geniuses) might have been mocked and ruined in the rear seats of their classes.

One aftermath of the acquisitive style of education within the biological sciences relates to statistics. Numerical skills, to measure quantities and their uncertainty, have become the cornerstone of modern science. And statistics are intimately linked to creativity because analysing data is one of the core activities to think, construct, evidence and communicate new ideas. Regrettably, mathematical training is in a precarious state in our field, due to a disconnection between the quantitative nature of ecology and the skills of mentors and students (Ellison & Dennis 2010). Johnson *et al.* (2001) have eloquently argued that 'wildlifers' who either lack or master statistical knowledge always walk on safe ground; because the former rely on experts to do their analyses, whilst the latter work out their numerical riddles by themselves (**Figure 1**). In contrast, the vast majority of scholars, across all levels of expertise, dwells in a statistical limbo prone to ill application, inference and/or reporting. Poor statistical training explains why most biologists that reach a postgraduate level are faced by a stunning contradiction: **Their hosting institutions expect them to have a solid mathematical background which, nonetheless, they most often never received**. I say 'expect' because, upon postgraduate enrolment, no procedure is generally in place to directly gauge an individual's practical skills with the methodological requirements of their intended projects.

Figure 1. Relationship between how well biologists use statistical methods (performance) relative to how much statistical expertise they have (knowledge). Performance is understood as one minus the probability of making a fatal statistical mistake (modified from Johnson *et al.* 2001).

Foreword

When the postgraduate researcher has had little statistical training, his/her study is doomed to drift into a do-it-your-self crusade. Some postgraduates will pretend to oversee their statistical weakness until they have collected their very final datum before entering into a state of acute concern when the time has come for wrestling with understanding and analysing their data. For others (I am one of them), such concern is chronic and they combat it by allocating resources and time to fill their statistical gap (e.g., courses, books), which can only ever be filled minimally given the demanding workload of a Masters or PhD. Fortunately, many postgraduates will survive the malady of numbers and get their degrees, although their struggle will simply perpetuate the demise of numerical training through the chain of education providers. I think that **a student can be intellectually dull or brilliant but, if he/she works hard, an adequate provision of statistical training and mentorship is the sole responsibility of the education providers**. Universities could have stringent criteria to accept only students with top statistical proficiency — but, as mentioned before, there would be too few who fitted the bill. The alternative, and most humane option, is *simply* delivering the training that is missing through the entire process of education. Excellent universities and excellent schools can only provide the best of their societal services, not in isolation but as parts of an excellent holistic education; that is a system that integrates all the phases of academic formation since the child sees a number or a letter for the first time until the adult might become a Nobel laureate.

As I finalise this foreword, my mind pounds ‘science is a point of view’, so we are not born with it and it requires dedicated learning… and teaching.

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