



OPINION PAPER

# Why we need a Canonical Ecology Curriculum

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## Abstract

As commonly perceived and pointed out, ecology is fragmented into many poorly integrated subdisciplines, resulting in recruiting, communication, and perspective meta-problems. To put together those fragments, solve those meta-problems, and integrate our efforts more efficiently we suggest a tentative Canonical Ecology Curriculum to be used for training the next generations of ecologists. Such a curriculum should be structured around a backbone of robust theories, classical case studies, and common methods, which we can expect to be taught in any graduate programme worldwide. This would minimise the ambiguity of what an ecologist learns in different countries and continents, strengthen our common vocabulary for internal communication, and help us bridge basic and applied Ecology more efficiently. This minimalistic backbone would leave plenty of room for the “free programme”, so that each institution also teaches knowledge and skills relevant to its own reality. To achieve this aim, we propose to focus on eight spatiotemporal scales, very much in line with current textbooks, but in reverse order: from global to genetic. This would be consistent with our ability to understand and predict, as aggregated entities average out the idiosyncrasies of lower organisational levels. We close on a call for global collaboration to exchange experiences, define common goals, develop the curriculum, and operationalise its use for real-world teaching.

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<sup>\*</sup>“The road is long, with many a winding turn.” Scott & Russell (1969)

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## Introduction

It is my first visit to a Namibian waterhole. A kudu drinks but remains vigilant. It tolerates a few duikers and even a skittish warthog by its side. But as a male nyala approaches, the kudu scares it away with a few aggressive snuffles. Sure: kudu and nyala are too alike in their body size, violating Hutchinson's 4/3-body-size-ratio rule of competition (Hutchinson, 1959; but see Eadie et al., 1987). Ah, isn't it great to be an ecologist!

But what does it actually mean to be an ecologist? Do we possess some consistent knowledge of our world? Do even two people with a Ph.D. in ecology from different universities share common knowledge and skills?

We believe that “ecologist” and “Ecology” (with a capital E to indicate the scientific discipline) are more than labels, despite collecting a broad range of scientific activities, attitudes, competences, skills, backgrounds, and goals. Ecology is a natural science with its own research agenda, even though with every new funding call, technological advance or policy drive, new marginal fields seem to spring into being. Such a diversity of mindsets and approaches is a great asset to our discipline, but also puts us at risk of losing the common ground if we do not foment at least some degree of integration.

Bearing integration in mind, our goal by writing this opinion piece is to share our impressions and aspirations with as many colleagues as possible, so we also get to know your own impressions and aspirations. By sharing our feelings, we can hopefully ignite a global discussion about the training of young ecologists. Through this discussion, we want to stimulate our community to rethink how we teach Ecology by focussing on what can be generalised (Dodds, 2009) rather than on anecdotes. As a side effect, we believe this exercise will increase exchange and strengthen the common ground between ecological subdisciplines. Most importantly, to be fruitful this exercise needs to be jointly conducted by people from different countries and continents, with different worldviews, who face different realities, so we can promote also within Ecology the diversity we so cherish in nature.

This opinion piece is inevitably biased by our own personal experience interacting with students, postdocs, consultants, analysts, policy-makers, stakeholders, traditional communities, indigenous communities, researchers, lecturers, and professors from different countries. We cherish the diversity of worldviews found among fellow ecologists and do not want to impose our own. Rather, we want to promote a deep, global collaboration, through which we might tell apart idiosyncrasies from shared problems, impressions from evidence-backed interpretations, and local from global goals. In the end, we want to work together to define operational goals, develop science-based solutions, and share resources.

We want to begin by motivating our community to work together in building a small but Canonical Ecology

Curriculum, so we start by explaining how it might help to solve three meta-problems that cause the fragmentation of our discipline, as perceived by many of us<sup>1</sup>. Next, we outline tentative steps towards agreeing on the minimal content of the curriculum, and how it can also help bridge basic and applied Ecology. We close on some concrete steps to be taken by the international community to jointly deliberate and facilitate the development of such a curriculum.

## Three meta-problems of ecology

The lack of a minimal integration within Ecology may well affect the quality of our science. Even at a higher level, it creates at least three “meta-problems”: (1) what to expect when recruiting?; (2) what do we mean by a technical term?; and (3) what do we actually know?

## The recruiting problem

Filling an open Ph.D. position in Ecology is becoming more and more challenging. It is not only because people are lured away by better pay outside academia, although peripheral countries with inflation-corroded scholarships face a debilitating brain-drain (Guedes et al., 2023). Also, it is not because potential students mistake ecological science for environmental activism. Rather, the main reason is that we have no idea what a recruit can be expected to know about Ecology. The cutting edge of research, in Ecology as in any other scientific discipline, is several steps ahead of the baseline knowledge and skill set of students finishing their degrees (typically, a B.Sc. or M.Sc.). Therefore, taking on a Ph.D. student inevitably involves substantial “training on the job”. But what does a new doctoral candidate have to learn, and what can we assume they already know?

We have the impression that ecological training is very fragmented and inconsistent. Recruiting ecologists globally comes with substantial uncertainty: What exactly did they learn when studying Ecology in San Francisco, Santiago de Chile, São Paulo, Sevilla, Shanghai, Soweto or Stuttgart? Studying economics, physics or medicine will certainly also differ between universities from different cities, countries or continents. Nevertheless, any economist will know supply-demand theory, any physicist will have read optics, and any medical student will know the names of the 206 bones in our bodies. Our personal experience after decades in the classroom shows that, in Ecology, we cannot even assume graduates to have understood the theory of predator-prey dynamics according to Lotka-Volterra or to know the biogeographic realms of the world.

Beyond their actual ecological knowledge, are students able to appreciate the interdependence between theory and

<sup>1</sup>See an informal poll at <https://dynamicecology.wordpress.com/2017/09/26/is-ecology-a-single-scientific-discipline/>

practice? The scientific method (as detailed for ecologists by Ford, 2000) is imbued in any physical or biological study, but Ecology straddles the basic-applied science discontinuity, often mixing politics into science (Horton et al., 2015; Maier & Feest, 2016; Montoya et al., 2018; Oliver & Cairney, 2019). Given the high degree of inconsistency in training, the three vertices of Ecology (theory, experimentation, and natural history) are often considered complementary, rather than integrated. As observed by many colleagues and us, in general, students with decent grasp of natural history are happy to declare themselves ignorant of theory and experimental skills, while more theory-bound students usually have a hard time designing experiments, and so forth. Naturally, a good student can be more theory- or practice-oriented in their way of doing science. But even theoretical ecologists need experience in the real world, so that their work links to actual systems. Likewise, empirical ecologists also need to be educated in theory, so they learn how to put field or lab observations and experiments into context and deduce expectations from larger bodies of knowledge.

In addition, depending on the combination of textbooks and professors they were exposed to, students are more in line with an evolutionary, organismic or systemic approach to ecological problems. Sadly, that favourite approach is seldom problem- or theory-oriented, virtually never epistemologically robust, and often the proverbial hammer to which everything looks like a nail. A Canonical Ecology Curriculum might help weave a red thread through approaches and contents.

## The communication problem

Every discipline uses technical terms: the so-called jargon. That is perfectly natural, not only in science but also in any human culture, as people who spend a lot of time together working on a subject develop their own efficient dialect. Actually, some jargon is very useful, as it makes for precise internal communication. A term such as “allopatric speciation” conjures a specific mental image within evolutionary ecology. Other jargon, though, is mere chatter. Telling one from the other is difficult for fledging (and fully fledged) ecologists. Worse, buzzwords used to pull the skin over the eyes of funding agencies may be perceived by others as real, operationalised scientific concepts. Some ambiguity will probably always persist (Grimm & Wissel, 1997). Nevertheless, it is counterproductive when we re-define terms as we see fit, thereby creating the illusion of a link to the existing literature, when in fact they refer to something entirely different (see Fauth et al., 1996 for an ignored attempt of sanitisation).

Students, usually encouraged by confused professionals, do not realise that the term “biodiversity” was coined for communication outside Ecology (by Walter Rosen for the National Forum on BioDiversity: Wilson, 1988), and wrongly believe that there is a coherent “biodiversity

theory.” As a result, they use “biodiversity” as a proxy for taxonomic distinctness, phylogenetic diversity, functional diversity, richness, evenness, abundance, and nature itself, among a myriad of concepts, clouding their thinking and writing. This is much more serious than sloppy reading. It points, in our view, to a misunderstanding of the difference between buzzwords used for selling projects and real scientific concepts that represent bodies of knowledge. One symptom of this confusion is the inability of many students to argue causally when asked “What is so good about biodiversity?” (Maier, 2012). Their confused minds resort to fallacies such as *argumentum ab auctoritate* (“Wilson said so”) or *argumentum ad consequentiam* (“If there were no positive effects of biodiversity, all struggle for conservation would be useless, and that cannot be”).

Another common behaviour, among professionals as much as students, is to claim an effect (for instance, of nutrients) on “biodiversity”, but when failing to find a correlation between the chosen factor and species richness, to quickly move through the above list in order to demonstrate that some other type of “biodiversity” is affected. That is not only intellectually unsatisfactory, but also philosophically and statistically wrong, due to unsound operationalisation. Students should comprehend the intricate cognitive maps woven around those meta-concepts before learning how to calculate metrics or plot graphs.

Values are key to integrate any human culture, and scientific disciplines such as Ecology are human cultures, after all. The communication problem will take a long time to resolve, but one way to start is by harmonising what is taught to the next generations. A Canonical Ecology Curriculum may also foster greater harmonisation among those teaching and practising ecology.

## The perspective problem

Theory, in ecology and elsewhere in science, is a serious, forward-looking, science-rallying, central condensation point of data and ideas. In a post-truth society, not only relationships, but also ideas became liquid (*sensu* Bauman, 2000). Ecology is no different, so there is no shortage in statements labelled “theory” in our discipline (Palmer, 1994, recorded several dozen for species richness alone), varying widely in experimental support. focussing our teaching on ideas that survived testing, our impression is that many studies employ theories as a coat-hanger for data in the publication narrative. Unless we keep good track of the key concepts and challenges addressed, corroborated and rejected, we will keep returning to them unproductively over and over again (Fox, 2013).

Precisely because we do not study or teach our common past in a consistent way, ecologists reinvent one wheel a day. It is quite usual to see them claiming in top journals to have “discovered that” or “invented this”. However, after a

quick search in the main scientific databases, sometimes you find that some novelties are old wine in new bottles (Belovsky et al., 2004). Similarly, logically consistent arguments that terminated entire lines of research decades ago (Connell's (1980) arguments against coevolutionary competitive displacement; or Hurlbert's (1971) critique of species diversity) are now forgotten and the abandoned research resurfaces without resolving the original issues. As a consequence, there are many vital questions remaining unanswered in ecology (Sutherland et al., 2013), resurfacing from time to time (Belovsky et al., 2004).

Dead-ends abound, and with thousands of new ecological publications per year, it is impossible to keep up. And there is no incentive for any journal, publisher or scientist to collect and relate publications. As long as we can claim in article introductions that “not much is known about” this or that, flying in the face of a century of research in related topics just under a different name, why should anybody make an effort to be thorough? One of the few highlights in recent conceptual synthesis is the Herculean work by Velend (2010, 2016), who related dozens of “theories” about guild organisation (what he calls “horizontal communities”) and connected them to one another using four meta-processes (selection, drift, dispersal, and speciation). There are other outstanding examples of colleagues working to provide Ecology with better tools for conceptual synthesis, bearing in mind that those tools must have a strong analytical (Nakagawa et al., 2019) and philosophical (Travassos-Britto et al., 2021) basis.

Considering this lack of historical perspective, we should be very circumspect whenever we read (or write!) that a given topic is poorly studied (Jaynes' Mind Projection Fallacy: just because I don't know, it doesn't mean it is not known). Often it may be a genuine lack of abstraction to relate a specific observation or experiment to other fields of research, not a lack of relatable publications. Maybe that happens because top ecological journals put emphasis on novelty, also expecting citations to be made of a bulk of recently published papers to boost impact factors. Why should we regard what previous researchers thought when only papers published in top journals in the past five years are considered relevant science? A Canonical Ecology Curriculum might help put ideas and evidence into perspective.

## Why should a Canonical Ecology Curriculum solve these problems?

The recruiting, communication, and perspective meta-problems outlined in the previous sections represent crucial challenges in Ecology. We argue that a Canonical Ecology Curriculum will address them to a large degree. Before we make some first suggestions about what such a curriculum should look like, we would like to justify our proposed solution.

Firstly, in our view, those problems have grown so large over several decades, that they cannot be fixed within a few years. Rather, it will be a generational task to develop a more mature foundation for Ecology. Thus, teaching the next generations of ecologists is a logical starting point.

Secondly, teaching means deciding what to include and what to omit. This selection pressure forces us to reject elements of ecological folklore that are dispensable. Often this will be because these elements are redundant or idiosyncratic. If we can brilliantly illustrate the idea of keystone species with otters and kelp (Estes & Palmisano, 1974), we do not have to also use starfish (Paine, 1966) and sharks (Ferretti et al., 2010) and elephants (Rietkerk & van de Koppel, 1997). That might only lead to confounding this concept with ecosystem engineers (de Visser et al., 2013) or losing the focus due to experimental design issues (Hurlbert, 1984). It is a matter of didactic clarity which anecdote to use as an illustration. Historic precedence is not really the most relevant aspect in this particular case, although we should always point students to who said what first in order to teach them that scientific knowledge is not static but a temporal, collective construction. In addition, it is important to consider the local reality of each institution, when deciding which examples should be added to the key example, in order to provide the curriculum with a local flavour and contextual learning.

Third, we will spend less time on miscommunication when we have common language, theory, and references. If it can be assumed that all ecologists know the theory of predator-prey dynamics according to Lotka-Volterra and are familiar with the classic case study on the snowshoe hare-lynx cycle, we have a more advanced starting point than current presentations at ecological conferences.

Fourth, a Canonical Ecology Curriculum requires lecturers around the world to be very familiar with the contents and skills they teach. This way, it will not be a lottery what students are taught. If the curriculum contains experimentation with bacteria as a model system, even theoreticians have to get their pipettes wet. Similarly, monitoring experts will need to be able to teach the mathematics of the Janzen-Connell-effect. This will create much more overlap in competences and experiences by ecologists at all academic levels, which we regard as a crucial basis for better scientific exchange. Practically, this requires making available and sharing good teaching material openly to reduce preparation effort.

Admittedly, it would be impossible to cover the basics for all topics relevant to our discipline. We are talking about a scientific challenge that dwarfs those of physics or chemistry, our role model “hard” sciences. Any attempt to teach *all* of Ecology is doomed right from the get-go. The best we can do is to try to agree on a minimal curriculum. Such a curriculum would not aim to comprise all topics studied by all ecologists in all institutions at all times. It would rather focus on the minimum content that makes Ecology coherent. In other words, the foundations that define Ecology as an



independent scientific discipline: the backbone of our science. To this curriculum each graduate school should add its local flavour, in order to engage students by using their local realities as examples (again, contextual learning is crucial), and raise their awareness to environmental problems faced by their own societies.

## Towards a Canonical Ecology Curriculum

A Canonical Ecology Curriculum would focus on the backbone of the body of knowledge shared by contemporary ecologists all over the world. As such, it will be able to provide a basis for ecological research, strengthening the foundations from which to reach the frontiers of our discipline.

However, in contrast to much older disciplines such as law, medicine or physics, in Ecology this backbone is not obvious and articulated. Many pages in go-to textbooks of our discipline are filled with illustrative anecdotes, seemingly culminating in an attitude of “everything in ecology is idiosyncratic” and “context-dependent” (Keller & Golley, 2000 is devoted to exploring why this is and how to still pull Ecology together philosophically). And it seems undeniable that ecological research finds variability far more often than constancy. Thus, we suggest that a Canonical Ecology Curriculum should contain three core elements:

- (i) a conceptual backbone of theories, frameworks, laws, rules, and principles;
- (ii) a list of classical case studies that built our foundations and serve as role models; and
- (iii) a methodological tool set that comprises the most common approaches to generating ecological knowledge, be it observational, experimental or theoretical.

Inevitably, a Canonical Ecology Curriculum would be dynamic as any other curriculum, so it would benefit from a continuous, structured, collaborative development among ecologists. Also, its local implementation will require many additional elements, depending on the interests, competences, and resources of each institution. We believe that such a curriculum would be the staple food, nutritive but bland, which needs to be enriched and spiced-up by enthusiasm, hands-on experience, and local examples and research interests of students, lecturers, researchers, and professors. Thus, while proposing such a Canonical Ecology Curriculum, we try to keep it minimalistic, in order to make it as engaging and interesting as possible by leaving plenty of space for the “free programme.” The local free programme is as important as the backbone for training young ecologists, also to reduce biases accumulated in our discipline, which stem from neo-colonialism and other forms of prejudice (Konno et al., 2020; Trisos et al., 2021), and worsen the three meta-problems discussed in the beginning.

A first, crucial step is to define the goal of Ecology. Unfortunately, that is no easy task (Cooper, 2003), as definitions of Ecology abound in the literature since the 19<sup>th</sup>

century, when Haeckel first baptised our discipline (McIntosh, 1986). We here combine the two main definitions by Haeckel (1866) and Andrewartha (1954), and state tentatively that *ecology is the study of the relationship between organisms and environment in order to understand their abundance and distribution*. Odum’s (1953) ecosystem-based definition is implied in this one (Scheiner & Willig, 2008). Naturally, our definition is not consensual, precisely because of the fragmentation of Ecology as a discipline, and therefore it also needs to be collectively discussed and refined when developing the curriculum. At this moment, based on this tentative definition we may draw a curiosity-driven, fundamental research agenda, which forms the basis of both basic and applied Ecology (Courchamp et al., 2015).

Core to ecological research are its two fundamental equations, one for populations, one for communities, described in shockingly trivial form. First, the population dynamics of any species may be modeled as (e.g. Hutchinson, 1978, also known in teaching as the “BIDE” equation):

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

where  $N_{t+1}$  is the population size at time  $t+1$ ,  $N_t$  is the population size at time  $t$ ,  $B_t$  is the number of births at time  $t$ ,  $D_t$  is the number of deaths at time  $t$ ,  $I_t$  is the number of individual immigrants at time  $t$ , and  $E_t$  is the number of individual emigrants at time  $t$ .

Second, the dynamics of the number of species in an ecological community can be seen in a very similar way (e.g. MacArthur & Wilson, 1967):

$$S_{t+1} = S_t + Spe_t - Ext_t + I_t - E_t,$$

where  $S_{t+1}$  is the number of species in the community at time  $t+1$ ,  $S_t$  is the number of species in the community at time  $t$ ,  $Spe$  is the number of species gained by speciation,  $Ext$  is the number of species lost by extinction,  $I_t$  is the number of immigrant species at time  $t$ , and  $E_t$  is the number of emigrant species at time  $t$ .

Those equations contain pointers to most fields of ecology:  $B$  and  $D$  are the focus of population ecology,  $I$  and  $E$  are the focus of landscape ecology and biogeography,  $Spe$  is a central topic in evolutionary ecology, and  $Ext$  is a cornerstone of conservation.

But similarly, we should be able to link any ecological research back to the processes encapsulated by these equations. Ecosystem ecology describes (among other things) the availability of energy and nutrients, which co-determine  $B$  and  $D$ . Food web ecology describes who eats whom, and hence similarly links back to  $B$  and  $D$ . A corollary of this viewpoint is that any field of Ecology that describes pattern for their own sake risks irrelevance. If, say, a network study were to only describe network topologies it may well be Mathematics, but not Ecology, unless it links back to these fundamental processes. For instance, by proposing how network specialisation might reduce competition and, hence, mortality ( $D$ ) in an interacting population.

Moreover, the fundamental equations, by nature of being equations, force us to quantify the contribution of different factors. Finding that tree roots exchange “some” nutrients through mycorrhiza between species is not *per se* relevant to Ecology (Karst et al., 2023); but it is when it scales to amounts relevant for growth or survival, or if it affects induced defences or drought resistance. When humans “harvest” forests, cereal fields, and ungulates, often this dwarfs any other cause of mortality, which is of course of practical relevance when addressing applied questions by means of scientific reasoning.

Arguably, the aggregated properties of a system are easier to predict, so we propose to think of a Canonical Ecology Curriculum from large to small scales, in contrast to most textbooks. In addition, processes shared between systems are probably less difficult to understand than idiosyncratic phenomena. So, we suggest focussing on very broad patterns at each spatiotemporal scale, and going down from ecosystems to communities to individuals to genes (Table 1).

Our proposal has three core elements of *what* to teach: theories and frameworks, classical case studies, and main methods used to acquire information (*in natura*, *in laboratorio* and *in silico*). Arguably, these core elements would only become a complete training programme in combination with complementary topics of paramount importance, such as the scientific method (to understand why inductive case study generalisations are problematic, as is data collection without an underlying theory), logics (to learn how to build valid, cogent arguments), algebra (for any quantitative approach really), data science (including data curation, visualisation, analysis and the FAIR principles), written and oral communication (to learn how to effectively convince audiences and pierce through smokescreen buzzwords, especially for papers and talks), taxonomy and systematics (for understanding the intricacies of what a “species” is and being able to identify one), computer labs, physiology labs, and, last but not least, field courses and excursions. Anyway, although we must be able to expect every person with a B. Sc. or M.Sc. in Ecology to have been taught, say, the Janzen-Connell effect, it matters much less whether they visited the Central Kalahari Game Reserve or Poço das Antas Biological Reserve, or looked at acacia or fig trees, no matter how gorgeous they are, to see that effect in action. Although it matters considerably for contextual learning.

Allow us explain in more detail what we mean by each core element:

Theories and frameworks are rare in ecological studies (around 50%), compared, for example, to those in experimental physics (>90%: Schneider, 2009, p. 10). They are also often specific to spatio-temporal scales, i.e. ecological levels of organisation, hence the common arrangement of ecology textbooks from individual to ecosystem (remember your classes based on Begon/Harper/Townsend, Beeby/Brennan, Krebs, Pianka, or Ricklefs). We suggest reverting this sequence, as it seems that our ability to understand and

predict system behaviour is better at coarse scales and gets evermore idiosyncratic towards fine scales. Confusingly, ideas, concepts, and frameworks proposed by theoretical studies may have been called “models”, “paradigms”, “hypotheses”, “laws”, “rules” or “theories”, without real care for what those philosophical terms imply. We might, for now, go with the pragmatic definition of Dodds (2009): “A statement about a mechanism that is mostly true” (Platt, 1964; Peters, 1991; Travassos-Britto et al., 2021b, but see O’Hara, 2005 for arguments against searching for laws in ecology). Often, we are able to boil down this myriad of “theories” to a thicker set of underlying cognitive maps. For example, we can directly connect the “keystone species concept” to the more general frameworks of food webs and important species (Mello, 2020). This could stem the proliferation of ever new, highly specific “theories” (see Vellend 2016 for a better elaboration of this argument). In the past decades, there have been some efforts to compile and organise ecological theories and frameworks, which provide us with a nice starting point for the theory element of the Canonical Ecology Curriculum (see in particular Dodds, 2009; Pasztor et al., 2016; Scheiner & Willig, 2011; Schneider, 2009 for some out-of-the-box examples). In contrast to physics, ecological entities are heterogeneous, i.e., distinguishably non-identical, which makes deriving laws in a similar way much more difficult (Elsasser, 1981; Ulano-wicz, 2011). Aggregates, however, can still be described, to some extent, by general rules.

Classics are case studies ruminated in textbooks, which founded our main research programmes in Ecology. Sadly, there seems to be a tendency, in Biology as much as in Ecology, to teach the charismatic exception (think of Darwin’s hawkmoth *Xanthopan morgani* as example of a specialised pollinator, when in fact the vast majority of pollinators are generalised). That is problematic, as it may create in our students an impression of inexplicability, lack of pattern, idiosyncrasy. Classical case studies probably should be selected to demonstrate what happens more often than not. Luckily, this is what happens particularly in shorter ecology textbooks (Beeby & Brennan, 2004; Nentwig et al., 2004; Odum & Barrett, 2004). Classics should be independent of the particular system at hand, in other words, they should be based on transferable assumptions and, so, be generalisable. And, ideally, they should be referable to with a simple label, e.g. “the snowshoe-hare-lynx cycle”. There are plenty of such classics around, and it will be hard to narrow them down to a few per scale. But we think it is necessary for reasons of homogenising our backbone. Comprehensive lists with broader selections may be found in some books (Miller & Travis, 2022; Real & Brown, 1991) and papers (Couchamp & Bradshaw, 2018), which do also provide us with a starting point. Nevertheless, we need to pay attention to worrisome cognitive biases, when putting together those reading lists, so we do not repeat the same mistakes all over again, especially underrepresentation of classical studies outside the mainstream literature from central countries.

**Table 1.** A tentative, minimalistic version of the Canonical Ecology Curriculum organised by scale (large to small), considering some main theories or frameworks that connect ideas and data, classical studies that founded each research program, and the main methods used to produce knowledge. These are just examples and most certainly neither complete nor optimal. The curriculum is supposed to be developed through an intensive, global collaboration, using online platforms and in-person workshops, with input from ecologists from different countries and continents, who have different worldviews and face different realities.

Scale	Target variables (examples)	Theory or Framework	Classics (by keyword)	Methods
Global	Biomass production; species density; functional richness	Biogeography; Macroecology; Bergman's rule; Rapoport's rule; global gradients of species richness; How many species are there?	Island Biogeography; Macroecology	Databases; linearized mixed-effects models; non-linear models; additive models; basic algebra
Landscape	Patch-level population size	Landscape structure (= composition + configuration); meta-community; meta-population; species-area law; landscape networks; conservation	SLOSS; fragmentation; metapopulations; meta-community concept; landscape networks	GIS; remote sensing; biotelemetry; mathematical modelling
Ecosystem	C-, N-, P-pools and fluxes; water fluxes; decomposition rates; tree growth; energy density per trophic level	Nutrient cycles; energy fluxes	Biosphere 2; Duke & Harvard Forest; FLUXNET	EC-towers; decomposition bags; leaf chemistry; Earth system models; forester diagram-models (ordinary differential equations: ODE)
Community	Species abundance distributions; co-occurrence patterns; network indices	Food webs; ecological networks; neutral theory; community theory; Janzen-Connell effect	Community theory; keystone species; Janzen-Connell effect; neutral theory of biogeography	Vegetation records; meta-genomics; multivariate statistics; McPeck-ODEs; stochastic simulations; network science
Pairwise dynamics	Population sizes; reproductive output; parasitism rate	Lotka-Volterra competition, predation, and mutualism models; parasite-host dynamics; disease spread; allometric prey-predator rules	Snowshoe-hare-lynx; <i>Paramecium aurelia</i> vs <i>P. caudata</i>	Microbe experiments; predator monitoring, hunting trade monitoring, ODE simulations; game theory
Population	Population size; resource uptake rate; vital rates (growth, mortality, fertility)	Lotka-Volterra population dynamics models; Liebig's law of minimum; optimal foraging; self-thinning law; movement ecology paradigm	Loggerhead turtle; optimal foraging models; movement ecology paradigms	Mark-recapture; distance sampling; plot sampling; Leslie/Lefkovitch matrix models;
Individual	Activity budget; movement; feeding preferences; ontogenetic changes in behaviour	Individual specialisation; behavioural ecology; evolutionary game theory; allometric growth law; dynamic energy budget	Individual specialisation; evolution of altruistic behaviour; the logic of animal conflict	Biotelemetry; cafeteria trials; captivity experiments; mathematical modelling
Genes	Allele frequencies; heterozygosity	Population genetics (selection, mutation, genetic drift, gene flow); coalescent theory; landscape genetics; conservation	<i>Drosophila</i> and <i>Arabidopsis</i> ; Bottleneck effect; inbreeding depression; genetic drift	Behavioural observations; fitness manipulation; game theory; effective population size

SLOSS: single large or several small; ODE: ordinary differential equation; GIS: geographic information system; EC: eddy covariance; FLUXNET: consortium of EC-towers (<https://fluxnet.org/>)

Methods can be roughly divided into those carried out in the “real world”, be it in a lab, crop or preserve (*in natura*) or on a computer (*in silico*). Unless we learn how data are collected, through observation or experimentation, we will

lack an appreciation of their quality and the validity of the interpretations drawn from them. Indeed, we perceive some ecological data scientists currently as being too uncritical of the quality of the data that go into their analyses, many times

fitting sophisticated models to real-world noise. But that risk makes it even more important, on the methodological side, to be able to both mathematically “simulate a system” as well as statistically “analyse a system”. That facilitates teaching, as simulations are “forward” (from assumed parameters to simulated data), while statistics are “backwards” (from observed data to estimating parameters). The classical methods used by ecologists have been organised in books focused on field methods (Henderson, 2021; Krebs, 1998; Sutherland, 1996; Underwood, 1997) or computational methods (Case, 2000; Gotelli, 1995; Matthiopoulos, 2011; Stevens, 2009), providing us with excellent starting points.

## From basic to applied ecology

In many applied ecological questions, from conservation over biocontrol to nature-based solutions, the backbone covered by the Canonical Ecology Curriculum will be unable to give direct management advice. That is so because there are intermediate layers of translational science (*sensu* Courchamp et al., 2015) between the “naturalistic” and the “engineering” sides of Ecology. Consequently, we need to work to reinforce the bridges linking them.

Many applied studies work solely on the basis of experience, either formal (i.e., previous published results) or informal (i.e., personal, accumulated impressions). Solutions to applied problems are seldom based on principles, and meta-analyses synthesise applied results without linking them back to theories and frameworks, such as energy fluxes, nutrient stoichiometry or community assembly (Burivalova et al., 2019; Rey Benayas et al., 2009). In a “do as I say, don’t do as I do”-spirit, we can take an example of our own field: none of the recent reviews of the effect of agroforestry on “biodiversity”, coming to opposite conclusions, referred to actual ecological processes (see Mupepele et al. 2021, and references therein). In such cases, basic Ecology learns little from applied Ecology and vice-versa (Dayton & Sala, 2001; Scheiner & Willig, 2011), and both sides lose an outstanding opportunity for positive feedback.

Such feedback is crucial for building more solid foundations. For instance, when asking a colleague how many *Arctiinae* (tiger moths) we could expect in a given tropical location unknown to him, he argued that no theory exists to derive such a number (and we agree). However, having been told that there are 280 species of *Arctiinae* in a square kilometre in Peru, he could easily suggest several reasons for such a high diversity, mainly related to caterpillar specialisation in detoxifying different plant secondary compounds. This is quite common in Ecology: we have little to go on for prediction and are used to post-hoc speculation.

Clearly, some system features might remain unpredictable, such as the number of *Arctiinae* on a particular site. Nevertheless, equally clearly, we cannot claim ecological applications to work without demonstration of an ecologist’s

ability to quantitatively predict the outcome of an intervention, such as a restoration programme. To apply ecological principles, we first need to demonstrate that such principles (a) exist and (b) work for interventions. To do so, we must aim for much tighter quantitative links between management advice and ecological theory. We should also aim for more prominence of successful examples of “ecological engineering”.

This may well yield a severe disillusionment of our applied competences, should the number of reproducible, repeatable, gold-standard applications remain small for a while. But to us that is a better way forward than a few well-meaning experts declaring something to be a “standard”. Evaluation of effects is crucial to scientifically demonstrate competence, and validation rarely accompanies standard-defining documents.

## How to get there: a roadmap towards an international canonical ecology curriculum

A Canonical Ecology Curriculum has to emerge through collaboration and discussion, fostered mainly by academic societies, universities, and research institutes, but including several different social actors who have their skin in the game. A soft-incentive first step could be to introduce an “Ecologist” certificate, which would be awarded by scholar societies to those having covered the canonical content (not unlike ESA’s “4-dimensional ecology” education framework<sup>2</sup>, but with a stricter definition of content).

A second step could be to develop the Canonical Ecology Curriculum and link in existing material into *prêt-à-porter* package for graduate programs. Eventually, an obvious go-to place would be a Wikipedia page (“Teaching Ecology” or indeed “Canonical Ecology Curriculum”), which could help compile diverse resources to help teach the core elements proposed. It could collect links to textbooks, blog posts, video lectures, learning materials, computer labs, in-person and online courses, open excursions, open field courses, and similar resources (see Appendix for details).

A third step could be to develop dedicated teaching material missing from the previous step. As argued above, few universities will have the resources to teach all core elements, but some classes might be available as MOOC (massive open online courses) elsewhere. Some lecturers may share their material and allow it to be improved by others (open teaching), which would also help harmonise teaching. Some textbooks will do a particularly good job in explaining a specific element of the curriculum.

A fourth step could be to use workshops organized at international conferences to foster curriculum development as well as harmonisation of teaching activities. There probably needs to be a venue for discussing divergent preferences,

<sup>2</sup><https://www.esa.org/4dec/framework/#gsc.tab=0>



and a fine-grained scale of recommended curricular content. Over time, the diverging ideas of what is central to ecology, how much mathematics and natural history knowledge is essential, and how many principles and classics are worth teaching, will hopefully converge – because they work and have been socially validated.

Maybe we will end up with a list of principles similar to this one:<sup>3</sup>

- 1 Evolution organises ecological systems into hierarchies.
- 2 The sun is the ultimate source of energy for most ecosystems.
- 3 Organisms are *biochemical* machines that run on energy.
- 4 Chemical nutrients cycle repeatedly while energy flows through an ecosystem.
- 5  $dN/dt = \text{Birth} - \text{Death} + \text{Immigration} - \text{Emigration}$  (of individuals)
- 6  $dS/dt = \text{Speciation} - \text{Extinction} + \text{Immigration} - \text{Emigration}$  (of species)
- 7 Organisms interact—do things to each other—in ways that influence their abundance.
- 8 Ecosystems are organised into webs of interactions. (*Which rubs with 1.*)
- 9 Human populations have an outsized role in competing with, preying upon, and favouring other organisms.
- 10 Ecosystems provide essential services to human populations.

From each principle multiple hypotheses can be drawn, opening new avenues for research. Those hypotheses can then be operationalised using causal reasoning, so that they give birth to theory-oriented projects based on testable predictions. For example, that the sun is the ultimate source of energy does not directly translate into anything ecologists directly study, such as the population dynamics of a bird species in a meadow, species richness of Arctiinae in a cloud forest or bat-plant interactions in a savanna. The biochemical nature of processes is not relevant to speciation (principle 6) *unless* the causal chain linking these two processes is made visible. Principles are fundamental to any science, but they are only the starting point.

Principles 9 and 10 can be summed up as “Humans are part of the world’s ecosystems, both at the dealing and receiving ends”. That is how Michael Kaspari joins basic and applied Ecology, an idea also advocated by the father of the keystone species concept late in his career (Worm & Paine, 2016). An important step for Ecology could be to demonstrate that principles 1–8 can lead to management strategies that, when followed, offer solutions to environmental problems. Again, the causal reasoning of how these principles translate into relevant processes at the scale of application requires a strong theoretical backbone, as proposed in the Canonical Ecology Curriculum. Application needs more, not less, theory, but only theory that is able to provide explanations before a fact happens, not after it.

Note that we do not claim that these 10 principles are new or unknown to ecologists; our point is that whenever we reduce a theory down to these principles, we are arguably “building” a theory based on what we (think we) know.

One of several complications is that Ecology overlaps with other disciplines, such as Botany or Evolution. The latter typically looks at time scales much longer than those of Ecology. Still, any ecological system’s configuration is the combined product of evolution and environment, and so must be stable to small disturbances and mutations. If some romantic statement about species coexistence in an Eden-like system (say, the Serengeti) is made, our alarm should ring: how could such a coexistence be evolutionary stable? And, at the other extreme of the spectrum: Why should a large population not drift apart, fragmenting into ecologically diverse sub-populations? While evolution seems rather unpredictable, its forces are useful when considering the maintenance or restoration of ecological configurations.

## Research for a Canonical Ecology Curriculum

Hoping that our community agrees with the need for change, what tasks could contribute to a Canonical Ecology Curriculum in terms of scientific research? We see three tasks as vital to this enterprise: building theory, operationalising principles, and synthesising evidence.

Principles in Ecology, be either those listed above or elsewhere (Dodds, 2009; Lawton, 1999; Pasztor et al., 2016; Schneider, 2009), require operationalisation. Unless it is clear how to use a principle for solving a scientific problem, for instance by linking energy flux and biochemistry to speciation, they might be philosophically sound but scientifically useless. Operationalisation may take the shape of a flowchart-like procedural algorithm for addressing a problem or may result in a mathematical formulation (Kooijman, 2010). The first step is to link principles to problems by defining theoretical variables, their relationships, and which phenomenon they explain together. The second step is to think about the consequences of those relationships.

Each principle leads to a long list of logical consequences (as exemplified in Dodds, 2009). These need to be translated into hypotheses, from which we deduce predictions based on operational variables, which are then tested to indirectly evaluate the principle itself. Does evolution yield hierarchies in ecosystems? In theory, maybe, but in the real world? The point here is that some principles may be logically correct but ecologically irrelevant. The foundations of Ecology, and of a Canonical Ecology Curriculum, need to be as solid as possible, and hence the principles should be shaken, kicked, and battered as severely as possible to make sure they hold.

There is much work to be done to strengthen our foundations, as the vast majority of publications in Ecology today are either curiosity-driven or topic-oriented, but rarely theory-guided. The introductions of most ecological papers pay only lip-service to concepts and theories in a post-hockery, confirmation-biased way. Efforts at synthesising such studies typically remove the vast majority of them due to flaws in design or reproducibility (Gerstner et al., 2017). This indicates that (a) synthesis is really hard (O’Dea et al., 2021),

<sup>3</sup> Shamelessly nicked from <https://michaelkaspari.org/2017/07/17/the-ten-principles-of-ecology/>, italics added by us.

and (b) there is little reliable evidence due to poor study quality (Mupepele et al., 2016; Yang et al., 2022).

Still, synthesis with the aim of identifying which principles work, and which do not, is crucial for building up an understanding when we can and cannot use our discipline's body of knowledge to solve applied problems (Stewart, 2010). If, for instance, crop pest outbreaks remain unpredictable, so be it. It is better to know that than to believe in predictability but fail to deliver a solution to farmers, worsening problems related to food security. It is not only credibility towards decision-makers, stakeholders, and society that is being lost, but also brilliant students who turn away from a discipline that seems not to hold high scientific standards.

## Concluding remarks

This piece is yet another attempt to build a better Ecology, such as many before us (Belovsky et al., 2004; Dodds, 2009; Keller & Golley, 2000; Lange, 2005; Lawton, 1999; Marquet et al., 2014, 2015; O'Hara, 2005; Sutherland et al., 2013). Why should it succeed now, if it hasn't so far? One main reason is that international collaborative work has become much more common in recent years, not least thanks to the Covid-19 pandemic. Novel tools for online collaboration now abound, ranging from brainstorming to coding and writing. During the pandemic, lecturers and professors have looked around for, and produced, a wealth of online teaching material. And we have become more willing to share such material, not only with close colleagues, but with the wider world. It looks like the conditions are now suitable for a Canonical Ecology Curriculum to act as a condensation point of liquid ideas. That would help not only harmonise our teaching but also improve our communication and provide a stronger theoretical backbone for basic and applied research. A Canonical Ecology Curriculum would ideally be developed through discussion both within and between academic societies, which can support open, international sharing of knowledge and solutions for teaching Ecology. Most importantly, the quest for a Canonical Ecology Curriculum should be embraced by the younger generations of ecologists, as deep change is always intergenerational.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

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