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Always.

RÉSUMÉ

Au cours de la dernière décennie, la science est entrée dans une crise de réplication majeure, dans laquelle les principaux résultats de nombreux domaines de recherche se sont révélés impossibles à répliquer. Ce phénomène a engendré de nombreuses interrogations sur les fondements statistiques et éthiques de cette crise. En écologie, le problème est particulièrement aigu, car outre les problèmes statistiques et éthiques, nous sommes également confrontés à d'importants problèmes de contingence. La nature que nous observons à un point dans l'espace et le temps est le résultat d'une longue cascade d'interactions biotiques et abiotiques. Cela signifie que les choses que nous observons à un endroit donné sont rarement identiques à un autre point, même tout près. Les choses dépendent tellement de leur contexte en écologie que souvent, non seulement les valeurs des paramètres doivent être estimées localement pour un modèle donné, mais aussi les modèles eux-mêmes et les forces impliquées doivent souvent être remplacées.

De nombreux outils ont été proposés et développés pour améliorer la capacité de généralisation des études écologiques, y compris (mais sans s'y limiter) l'agrégation des données, la méta-analyse, la réplication à travers les régions et les écosystèmes, ainsi que les changements dans l'échelle d'observation. On pourrait également ajouter à cet ensemble d'outils techniques l'utilisation d'expériences par la pensée, comme de s’imaginer comment une mesure proposée pourrait être utilisée dans différents contextes, et quelles qualités une mesure devrait posséder pour être applicable dans le plus de contextes possibles.

Tous les outils ci-dessus sont des fardeaux supplémentaires sur les épaules des écologistes, ce qui peut nous amener à poser la question: cela en vaut-il la peine? Étant donné que si peu de lois écologiques fortes ont été découvertes jusqu'à maintenant, les espoirs sont également minces d'en trouver beaucoup plus dans l'avenir. Dans cette thèse, nous explorerons les avantages reliés à la

recherche de généralités dans les études écologiques, outre la découverte de lois générales elles-mêmes. Nous appliquerons ainsi les outils décrits ci-dessus dans six études, dans lesquelles nous tenterons de trouver des résultats généralisables à d’importantes questions écologiques, puis ferons une synthèse des avantages qui peuvent être tirés de cette quête de généralités.

Nous examinons d'abord les avantages de combiner la puissance de la science citoyenne de la base de données eBird dans l’étude de grands gradients spatiaux et temporels pour déterminer comment la structure des communautés d’oiseaux change au fil des saisons aux États-Unis d’Amérique. Ces résultats nous permettent de délimiter certaines régions où l’étude d’une communauté à un seul point dans le temps serait moins représentative de la communauté complète d’une année entière.

Nous examinons ensuite les avantages de combiner des bases de données entretenues par des professionnels (la base de données BioTIME) pour découvrir un lien entre l'abondance des espèces communes dans les communautés et la diversité de ces mêmes communautés, ce qui suggère que les deux quantités ne peuvent pas être maximisées simultanément, avec des implications importantes pour la conservation.

Troisièmement, nous examinons un exemple de méta-analyse, où la puissance statistique supplémentaire fournie par la combinaison de plusieurs études, nous aide à quantifier l'effet faible, mais tout de même présent, de la configuration du paysage sur la richesse en espèces lorsque l’on tient compte de la quantité d'habitat propice disponible dans le paysage. (c'est-à-dire l'hypothèse de la quantité d'habitat).

Ensuite, en combinant un modèle mathématique avec la télédétection à grande échelle, nous montrons le fort lien qui unit le couvert végétal et la variance de ce couvert à travers un gradient d'anthropisation, ce qui suggère que toute étude espérant explorer la relation entre l'une de ces deux variables et la richesse en espèces doit également tenir compte de la seconde variable, car sinon elle court le risque de confondre l’effet de l’une pour l’autre.

Nous combinons ensuite ces nouvelles connaissances avec un gradient forestier interécosystème, des méthodes de télédétection et d'évaluation rapide de la biodiversité pour séparer les facteurs affectant la richesse en espèces d'oiseaux dans les environnements forestiers de ceux qui proviennent uniquement de la corrélation entre les différentes variables environnementales.

Enfin, au moyen d'une expérience par la pensée, nous remettons en question la définition et les façons actuelles de mesurer l'intégrité écologique, en se demandant à quel point notre vision de l'intégrité écologique est toujours pertinente étant donné que notre monde change si rapidement et que les espoirs de revenir à des conditions précolonisation sont à peu près utopiques. Puis, armés de ce cadre conceptuel, nous combinons une fois de plus la puissance de l'agrégation des jeux de données et des approches de télédétection pour proposer une définition et des mesures alternatives d'intégrité écologique qui peuvent être utilisées pour comparer les communautés et les paysages à travers les biomes et les écosystèmes, un exploit que les définitions actuelles peuvent difficilement envisager.

Ainsi, cette thèse montre que l'idée de produire des généralisations en écologie est beaucoup plus riche que le processus, parfois simpliste, consistant à essayer de voir si les choses se passent toujours de la même manière partout. Comme illustré ci-dessus, il y a d’importants avantages à tirer de la recherche de règles générales en écologie. Pas nécessairement dans la découverte de ces règles comme tel, mais simplement par le processus de tenter d’en trouver. Entre autres, d’importantes questions écologiques et philosophiques peuvent être mises en lumière en tentant de mettre des choses côte à côte pour tenter de les comparer. Outre l'intégrité écologique, il existe aujourd'hui de nombreux sujets de ce type en écologie qui bénéficieraient grandement de ce genre de discussions. Peut-être que l’écologie ne trouvera pas de règles générales

comme on l’a espéré à une certaine époque, mais il est clair que la recherche de ces règles générales fera progresser la biologie et la conservation d’une manière plus nuancée et réfléchie.

Mots clés : Intégrité écologique, écologie du paysage, loi écologiques, écologie des communautés, crise de la réplication, évaluation des écosystèmes, synthèse de données

ABSTRACT

In the past decade, science has entered an important replication crisis, in which major results from many scientific domains turned out to be unreplicable. This phenomenon has engendered many questionings about the statistical and ethical underpinnings of this crisis. In ecology, the problem is even more acute because, in addition to statistical and ethical issues, we are also faced with important contingency problems. The nature we observe at a point in space and time is the result of a long cascading suite of biotic and abiotic interactions. This means that things we observe at one point are seldom identical in a nearby location. Things are so contingent on their context in ecology that oftentimes, not only parameter values need to be estimated locally for a given model, but also the models themselves and the forces involved need to be changed.

Many tools have been proposed and developed to improve the generalization capacity of ecological studies including (but not limited to) data aggregation, meta-analysis, replication across regions and ecosystems, as well as changes in the observation scale. One might also add to this set of technical tools the usage of thought experiments, such as imagining how a proposed measure could be used in different contexts, and what qualities a measure would need to become applicable across contexts.

All the above tools are additional burdens on the shoulders of ecologists, which begs the question : is it worth it? Given the fact that so few strong ecological laws have been discovered so far, the hopes are also slim of finding many more in the future. In this thesis, we will explore the side benefits of looking for generalities in ecological studies. We will thus apply the above list of tools in six studies in which we aim at finding generalizable results to important ecological questions, and then synthesize the benefits that were gained from looking for generalities in these studies.

We first look at the benefits of combining the power of citizen science in the eBird database with large spatial and temporal gradients to determine how bird community structure changes across seasons in the continental US. This allows us to pin-point particular areas in which a snapshot study at a single point in time is less representative of the year-round community.

We then look at the benefits of exploiting curated datasets (the BioTIME database) to uncover a link between the abundance of common species in communities and their respective diversity, suggesting that both quantities cannot be maximized at once, with important conservation implications.

Thirdly, we look at an example of applied meta-analysis, where the added power of combining multiple studies together helps us decipher the weak, but still existent, effect of habitat configuration on species richness when accounting for the amount of suitable habitat in the landscape (i.e. the habitat amount hypothesis).

Next, by combining a mathematical model with large scale remote sensing datasets, we uncover the very strong link between vegetation cover and land-cover variance across an anthropization gradient, which suggests that any study hoping to explore the relationship between one of these two variables and species richness needs to also account for the second variable, or else run the risk of mistaking one effect for the other.

We then combine this newfound knowledge with a cross-ecosystem forest gradient, remote sensing and rapid biodiversity assessment methods to untangle the drivers of bird species richness in forested environments.

Finally, by the means of a thought experiment, we challenge the current definition and measurements of ecological integrity, by asking how our current view of ecological integrity is still applicable given that our world is so rapidly changing and the hopes of reverting back to pristine conditions is more or less utopical. Then, armed with this framework, we combine once again the power

of aggregated datasets and remote sensing approaches to propose alternate definitions and measurements of ecological integrity that can be used to compare communities and landscapes across biomes and ecosystems, a feat current definitions can seldom envision.

The idea of producing generalizations in ecology is a much richer one than the simplistic process of trying to see if things always happen in the same way everywhere. As illustrated above, there are important insights to be gained from, not necessarily achieving general results, but by simply striving for them. There are very important ecological and philosophical questions that arise by putting things side by side. By comparing them and looking for common ways to assess them. Beside ecological integrity, there are many such topics in ecology today that would greatly benefit from these kinds of discussions. Maybe ecology won’t find general rules as was once hoped, but clearly, looking for them would make conservation biology progress in a more nuanced and thoughtful way.

Keywords : Ecological integrity, landscape ecology, ecological laws, community ecology, replication crisis, ecosystem assessment, data synthesis

INTRODUCTION

CONTEXT AND THESIS OVERVIEW

In the last decade, science has entered an unprecedented replication crisis (Baker, 2016). In almost every field, but especially in life and social sciences, a worrying proportion of high-impact studies have turned out to be impossible to replicate. The scientific method is classically described with the steps (1) observe, (2) question, (3) form an hypothesis, (4) make a prediction and (5) test that prediction. Although not explicit in that list, the fact that the test of the prediction can be replicated with similar results has always been an implicit tenet of the method. It is only through replication that one can build confidence about the hypothesis, and eventually construct knowledge.

Much thought has been given to the statistical underpinnings of the replication crisis. Null hypothesis testing has been highly criticized as one of the main culprits, mainly because it can be easily abused (often unconsciously) through both *p-hacking* (e.g. tweaking models until $p < 0.05$) and researchers degrees of freedom, (e.g. stopping data acquisition when statistical significance is reached, arbitrary subgroup analysis, etc). For instance, authors have found that researchers degrees of freedom alone could easily increase the false-discovery rate from the canonical 5 % up to an astonishing 60 % (Simmons et al., 2011). The initial plausibility of the tested hypothesis must also be taken into account while doing hypothesis-driven science, as the actual probability that an hypothesis is true after testing depends foremost on its prior probability before the experiment (Goodman, 2001)

One less explored aspect of the replication crisis is that conclusions from individual studies are often contingent on the study context. This problem is particularly acute in ecology, where having context-specific results is more the norm rather than the exception. At larger scales, basic theoretical models can often be tailored (i.e. parameterized) to the study-specific realities. But at smaller scales, especially in community ecology, the actual theories are often contingent upon the location or organisms studied (Lawton, 1999). When you combine these contingency issues with the fact that ecological results are more or less never replicated (Kelly, 2019), one can quickly realise why ecology fares so badly in terms of both replication and generalizations.

Many improvement areas have been suggested to alleviate these matters in ecology. In fact, a whole section will be devoted to them below, including data synthesis and scale changes. But upon reflecting on these strategies, one might wonder what is the point of adding all these constraints to the existing burden of conducting an ecological study, which often includes exhausting and costly fieldwork? Why should we keep looking for generalities, after finding so few of them after decades of trials?

This thesis will try to directly answer that particular question. We will illustrate the (often indirect) benefits of conducting ecological studies with the explicit goal of achieving generalizable results. Our plan involves three steps. First, the bottom half of this introduction will be devoted to the overview of the tools and techniques that can be used to improve our ability to generate general conclusions from ecological studies. Secondly, we will see six ecological studies in which these tools and techniques were successfully applied, and often combined. Lastly, in conclusion, we will synthesize the benefits achieved from the application of these techniques and give an outlook on the future of ecological generalizations.

GENERALIZATION THROUGH DATA SYNTHESIS

DATA AGGREGATION

One of the main issues causing unreplicable findings is the small sample size used in many studies. If the law of large numbers states that large samples should generate estimates that are close to their expected value, smaller samples on the other hand tend to show more important biases. Although null-hypothesis testing should alleviate part of that problem, *large* type I errors (e.g. typically 5 %) suggest that small sample sizes could still be part of the replication crisis problem.

Unfortunately, research budgets have not necessarily increased in the recent past and there are no signs they should do so in the near future either. This means that it will not necessarily be simple to increase the sample size of individual studies in the future.

Fortunately, the total amount of field work that has been completed since the beginnings of ecology keeps increasing. Depositing datasets in open repositories (DataDryad, FigShare) has become more the norm than exception and thus, the amount of data that is accessible to ecologists without leaving their desk has grown tremendously in the recent past. Nevertheless, these data are not necessarily easy to find nor easy to clean and reuse efficiently, but steps are taken in the right direction to address these issues (Wilkinson et al. 2016).

That is why curated datasets have become such a blessing for modern ecologists. When a group of scientists takes on the task of constructing an aggregated dataset that is easy to use, the usage of these datasets just skyrockets. For example, Dornelas' et al. (2018) BioTIME dataset, prepared to study biodiversity time series, has already been cited almost 80 times, despite not being even 2 years old. Once carefully curated, such datasets can be easily repurposed for many other usages. For instance, we used this dataset in Chapter 2 (see below) to quantify the compromise between diversity and abundance in thousands of communities worldwide.

An even larger new source of data has been the appearance of citizen science databases. At the leading front of this movement is eBird, a worldwide repository of bird checklists, to which more than 100 M bird sightings are added each year by amateur and professional ornithologists. Because of its sheer size and relative ease of access and reuse, the eBird database has been cited more than a 1000 times. More importantly, the constant influx of observations year-round can create study opportunities which would have been otherwise almost impossible to achieve. For example, in Chapter 1, the eBird dataset allowed me to study temporal trends in bird diversity across seasons for the whole continental US. Such a study would have been very hard even to consider without the concerted efforts of thousands of volunteers eBird has been able to gather. Many other projects are doing the same kind of aggregation work for butterflies (eButterly) or for the whole gamut of taxonomic variety (iNaturalist, GBIF).

Despite being highly curated, these datasets must still be used while keeping in mind some important caveats. These are especially important for citizen science projects. For example, distribution maps inferred from these databases are more often than not representative of human density (i.e. more human population means more samples) rather than actual organism density (e.g. Fig. S1 in Martin et al. 2018). Occidental countries/cultures are also much more present in these aggregated datasets, because of the language barrier between cultures that makes information exchanges difficult, as well as the importance of the academic structures, which varies tremendously between countries.

META-ANALYSIS

Gathering together data from multiple studies to run in a single analysis is not always a workable strategy. For instance, the farther you search in the past literature, the less likely it is that you'll have access to primary data used to produce the results. The practice of publishing data along scientific articles being a fairly recent one. That is why many ecologists have turned to synthesising research results from multiple sources, e.g. running a meta-analysis.

Meta-analysis involves the computation of a summary effect size, averaging the various individual effect-sizes found in the literature. This average is usually a weighted mean, that gives more emphasis to the more precise studies, and less to the smaller (potentially spurious) ones. Various elements can also be added to the model to account for both pseudo-replication and between study variation, either in the form of co-variables or random effects (Borenstein et al. 2009).

Meta-analyses are heavily used in medicine, where strict protocols have been established to define the correct procedures to conduct such a study. Organisations have been created specifically to gather, carry out and maintain meta-analyses (e.g. Cochrane).

Meta-analyses are also often used in ecology. They are particularly useful to put numbers on controversial theories and produce robust estimates to describe highly variable phenomena. Results are often less clear-cut than in medicine, because ecological results are often much more variable than medical trials where conditions are more controlled. More often than not, ecological meta-analyses must conclude by saying that between-study heterogeneity is very high and that there is no single canonical value that could synthesize the phenomenon at hand (e.g. Roca et al. 2016, Martin 2018, Brisson et al. 2020).

All caveats about data aggregation also apply to meta-analyses. Synthesising a sample biased toward temperate ecosystems will inevitably produce biased results in the same direction. In addition, one must be highly vigilant to the file drawer problem. There is a tendency, in any scientific field, to withhold the publication of (or to be outright unable to publish) controversial results that go against an established theory. Meta-analysis methods assume we are working with an unbiased sample of studies, which is rarely the case. Hopefully, techniques have been developed (e.g. funnel plots, Egger's test) to assess and quantify this "file drawer problem" (Borenstein et al. 2009).

GENERALIZATION THROUGH REPLICATION

REPLICATING ACROSS REGIONS AND ECOSYSTEMS

As discussed above, one of the main issues prohibiting ecologists from producing reproducible and generalizable conclusions is that more often than not, ecological experiments are small-scale case studies. Of course, there are myriads of reasons that could explain the massive production of small-scale case studies. There are important time and budget restrictions upon the realization of field studies. There are only so many summer days throughout a masters or a PhD. There are also many cases where there are just no sensible frameworks to connect multiple ecosystem types in a single, well-organized theoretical framework. Whether it is for logistical or conceptual reasons, ecological studies are often conducted with a relatively narrow scope.

However, in terms of generalities, there would be much to be gained by crossing ecosystem borders, testing in multiple climates, etc. For instance, conservation biology has made great strides by studying the contribution of beta diversity (i.e. species changes across space) to the gamma diversity of a region (e.g. the total number of species; Socolar et al. 2016). Crossing regions and ecosystems is also one of the (often implicit) benefits of data synthesis studies suggested in the previous section. This way of *a posteriori* stitching studies together comes with an important downside : authors have no control on the representation of specific biomes or ecosystem types. Synthesis are indeed often criticised specifically because they are mostly made of easy to study organisms in temperate climates from occidental regions. Only the proper planning of across-biomes or across-ecosystem studies could achieve an adequate sampling that would circumvent such issues.

WORKING AT LARGER SCALES

One way to rapidly add many sites to an ecological study and to cross ecosystem borders is to use remotely-sensed data. As hundreds of satellites are orbiting earth with various arrays of optical sensors, there are incredible amounts of data that are waiting at our fingertips to be analysed.

Nevertheless, the scale at which these data are gathered is often quite limiting, often in the order of hundreds of meters per pixel. This in turn limits the spatial grain that can be effectively used, and prohibits its usage for many taxonomic groups. Also, despite the fact that satellites generate terabytes of data every day, images from a single area are often far and few between, meaning that, combined to random cloud coverage, the pixels from an area of interest might be available only a couple of times per season, strongly limiting the possibilities to run daily or weekly analyses.

Whereas remote sensing is useful to study phenomena at larger spatial scales, there are also passive monitoring techniques that can be used to accomplish similar feats through time. These passive monitoring techniques can be employed to study both vegetation, through the use of time lapse cameras (e.g. Sonnentag et al. 2010), as well as sound-emitting animals, through the use of automated recording devices (see Chapter 5 for an applied example).

For relatively stable structures such as vegetation stands, the use of passive monitoring has opened the door to a whole new world of phenology studies. The amount of effort that would have been needed to visit a vegetation stand daily through months or years now can be reduced to a handful of visits, one to install and one to remove the camera, with an occasional check for battery and memory card states. With programmable audio recorders, the vocal activity at a series of sites can also be studied simultaneously. The advent of programmable audio recorders has pushed such techniques even farther, as now the time gradient can be automatically sampled at given intervals, which seriously reduces the amount of data generated and stored into the memory of these devices.

Although many ecological indices can be computally extracted from both vegetation images and audio recordings (Meyer & Neto, 2008; Sueur et al., 2014), there are also many tasks that need to be accomplished manually. For example, when studying songbird communities, there are still no automated ways to reliably identify all bird species in an audio recording. Consequently, the human part of the effort is not necessarily reduced when needing to work with precise species identifications. It is more or less transferred to the lab. The advantage in such cases is more a logistic one, where audio samples can be densely recorded during the short summer season in temperate climates, and then species from recordings can be identified in the lab during the winter months.

Whether we're thinking at increasing the scale spatially or temporally, the technological tools to do so are now readily available at fairly low costs, and have now become standard ecological methods, which are used in a variety of creative ways.

GENERALIZATION AND ECOLOGICAL INTEGRITY

All of the above generalization mechanisms are more or less statistical or technological tools. But this begs the question : are there *conceptual devices* we could use to look for generalities in conservation biology? One way we could do such a thing is by conducting thought experiments. By looking at concepts in a fresh way and asking ourselves : how general is this knowledge? Can it be applied in many places? In many contexts? In the following pages, we'll do that kind of thought experiment with a seemingly simple concept : ecological integrity.

To begin with, we will stick to the consensus definition of ecological integrity, which is often equated simply to *naturalness*. A typical definition usually reads like this : "Ecological integrity means [. . .] a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes” (Canada National Parks Act S.C. 2000, c. 32). Throughout the following sections, we will go through the typical ways in which ecological integrity is usually assessed and try to determine what are the shortcomings of these various methods. We will highlight the fact that one of the major hurdles for generality is the consensus definition itself, which we will try to refine and enhance in chapter 6.

Before going further, the terminology used to describe the conditions that ecosystems are experiencing will need to be clarified. One definitely controversial term in such a context is stress (Borics et al., 2013). Stress is sometimes defined as the cause (which some authors call stressor), sometimes it is defined as the response, and in some cases it is used for both meanings (Odum, 1985). In this thesis, we will define stress as any external pressure put on an ecosystem, that is to say, any changes in ambient conditions (e.g. temperature or nutrient changes, etc.) that would negatively affect growth. We’ll also define disturbance as any major event, through which important changes occur in the ecosystem, resulting in biomass losses (i.e. fires, hurricanes, etc., sensu Connell, 1978). Such a classification scheme aims to define the magnitude of an event, regardless of its origin (natural or anthropic) and whether its impact in the end is positive or negative for the ecosystem.

TAXON-BASED INDICATORS

A first group of frequently used ecological indicators can be gathered under the umbrella of taxon-based indicators. The principle behind these indicators is fairly simple : instead of measuring every detail from an ecosystem, the presence or relative abundance of one or a few species is used as a surrogate for the status of whole communities or ecosystems. The species are chosen either based on their ecological importance, their abundance, prior research or (disturbingly) without a clear justification in 17% of the cases (Siddig et al., 2016). Pioneered early in the 1980s for fish communities (Karr, 1981), taxon-based indicators were successfully applied to a diverse array of life-forms including diatoms (Van Dam et al., 1994), birds (O'Connell et al., 2000) and both aquatic and terrestrial invertebrates (Andersen & Majer, 2004; Barbour et al., 1996)

These indicators, although mandated in some regulations, have also been heavily criticized because of their discrepancy from ecological theory (e.g. resource partitioning, competitive exclusion, etc.), which leads to situations where the management of an indicator species can conflict with the management of others (see Simberloff, 1998 for examples). Other authors have also underlined that taxon-based indicators are based on unclear or missing causal mechanisms (Landres et al., 1988; Lindenmayer et al., 2000) and display variable levels of sensitivity (Hering et al., 2006, Chessman 2021).

COMMUNITIES

As taxon-based indicators are often restricted to specific locations, attempts have been made to generalize the concept using ratios of abundances of some animal guilds, based on life-history traits or trophic position. The root of these approaches can be traced back to E.P. Odum's work (e.g. Odum, 1969), where he developed a suite of ecosystem development indicators, that should transition throughout the development process (e.g. short vs. long life cycles, r-selection vs. K-selection, small vs. large body size, etc). An often cited example of this approach is Raffaelli and Mason's (1981) study, in which they studied the density ratios of nematodes to copepods on british beaches and showed that this ratio, although controlled by particle size, was also indicative of sewer pollution. Even though it is less tangled in species-specific issues, this guild ratio approach still received its fair share of criticism, especially because there are many instances where a guild responded both positively and negatively to disturbances depending on context (e.g. Gray et al., 2007). Some authors also argue that the guild concept itself, although conceptually appealing, is somewhat elusive and that guild definitions are mostly arbitrary (e.g. Hawkins & MacMahon, 1989).

More holistic approaches to the use of communities as ecological indicators have also been proposed, for example through the use of diversity metrics. Many diversity metrics are modified or extended versions of Shannon's entropy (1948), which includes aspects of both species richness and evenness (i.e. how hard is it to predict from which species comes a randomly picked individual). These numbers are known to go down in polluted or disturbed areas, but often lack the sensitivity necessary to detect small to medium changes in ecosystem conditions (see Jørgensen et al., 2005 for a review). Worryingly, empirical evidence for relationships between disturbance and diversity showed that about every possible shape exists (negative, positive, peaked, u-shaped, etc.; Mackey & Currie, 2001), suggesting that using diversity as a proxy to ecosystem state might not be as intuitive as one could expect.

HABITAT STRUCTURE

In parallel to what happened with trait-based ecology, which provided a workaround to the lack of generality of studies based on species identities by focusing on the species' characteristics (e.g. McGill et al., 2006; Violle et al., 2007), recent propositions have been made to use the physical structure of the vegetation as a complementary ecological indicator (Lindenmayer et al., 2000). Lindenmayer et al. (2000) identified three such structure types that should be of particular interest : stand complexity, connectivity and heterogeneity. The general idea behind structure-based indicators being that the preservation of the physical characteristics of the vegetation (or the mimicking of the structure of natural disturbances) should provision for the conservation of the underlying biodiversity (Attiwill, 1994; McComb et al., 1993; but see McElhinny et al., 2005).

Although promising, results thus far have been ambiguous, as organisms do not always respond coherently to differences in structures (e.g. Martin & Proulx, 2016; McAlpine & Eyre, 2002). Another strong argument against structured-based indicators is that, as of now, target structures have been defined from uncut stands, and thus depend on the existence of a pristine state somewhere to compare with (e.g. McComb et al., 1993).

ENERGETIC RATES

In his 1969 paper, E. P. Odum also proposed a series of development indicators based on system-wide energetic rates (e.g. production to respiration ratio [P/R], production per standing crop biomass etc. [P/B]) that should progress through ecosystem maturation. This idea was also present in Margalef's work (1963), where he stated that the relative amount of energy needed to maintain an ecosystem should be reduced as the system complexity increases.

These insights were highly integrative and provided valuable material for decades of ecosystem development indicator research (e.g. Christensen, 1995; Ludovisi et al., 2005; Pérez-España & Arreguín-Sánchez, 1999) but were also the subject of harsh criticism, being described, among others, as a “short-cut to a genuine understanding of ecological systems” (Fenchel, 1987). Extensions of these principles were nevertheless successfully related to disturbances on a limited set of lakes (Choi et al., 1999), but turned out to be difficult to test empirically at useful scales. Also, as formidable as Odum's and Margalef's intuitions were, these indicators were not based on formal theoretical models, so actual causal mechanisms are not directly provided.

ECOSYSTEM EXERGY THEORY

Many authors have also tried to construct ecological indicators from a more theoretical starting point. One such attempt is Schneider and Kay's (1994) ecosystem exergy theory, an extension of Schrödinger's (1944) idea that life could be studied as an open, far from equilibrium system, obeying to the second law of thermodynamics. According to this theory, life forms try to dissipate incoming exergy (useful energy) as efficiently as possible, and develop in a way that increases their ability to do so. It is thus expected that underdeveloped ecosystems (younger, more disturbed, etc.) should degrade exergy less efficiently than more mature ones.

Many indicators of exergy dissipation, mostly based on thermal measurements, have been proposed and successfully related to coarse increases in naturalness (i.e. buildings vs. gardens vs. forests) and forest maturity (Maes et al., 2011), as well as crop stress (Lawrence, 2016). Although this approach possesses many key features expected from an integrity indicator, it has one major drawback in that energy dissipation is clearly related to canopy height (Maes et al., 2011), complicating between-ecosystem comparisons.

The previous review makes it clear that no current indicators are at once realistically measurable and appropriate for among-ecosystem comparisons. Most of these comparison difficulties stem from the fact that none of the previous measures defines expectations for an ecosystem. Simple questions such as : “How much diversity should a temperate ecosystem contain?” or “What should a healthy respiration/biomass ratio should look like in the tropics?” have been so far unanswered.

If expectations were defined in an objective and context-agnostic way, it should open the door to between-ecosystem comparisons of ecological integrity. In turn, this would open the possibility for an emergency-style triage system, where ecosystem restoration and protection can be objectively prioritized. Conservation resources being finite, it always comes back to priority management.

CHAPTERS OVERVIEW

The following chapters will illustrate ways in which these strategies and observations can be applied to generate ecological knowledge that is more general and robust. Keep in mind while reading them that, although the hopeful goal of each study was to find general laws, the key is more in the path taken. In this thesis, it is mostly the side benefits rather than the goal itself that interests us. Specifically, Chapters 1 through 3 illustrates the advantages of using data synthesis techniques to provide general conclusions. Chapters 4 and 5 illustrate replication techniques whereas Chapter 6 combined both techniques (synthesis and replication) to explore the possible advances they could provide to the field of ecological integrity assessment.

CHAPTER 1

BIRD SEASONAL BETA-DIVERSITY IN THE CONTIGUOUS UNITED STATES

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Abstract

Beta-diversity, the measurement of community changes along gradients, is an important component of diversity, needed to understand how local communities are assembled from a regional pool. Although they have rarely been quantified, seasonal changes in species composition have important management implications, as they can hamper the representativeness of snapshot community studies. The present study thus maps bird seasonal changes in species composition (beta-diversity) across the contiguous United States, using weekly data from the eBird project. Besides management implications, this map also provides insights into the mechanisms driving seasonal beta-diversity, namely that it is mostly related to the annual temperature range and the size of the species pool.

Keywords: seasonality; turnover; migration; annual temperature range

INTRODUCTION

Beta-diversity is the measurement of community changes along gradients (Whittaker 1960). It is an important aspect of diversity, needed to understand how species are assembled from a regional species pool into a local community. Although community changes along environmental gradients are a highly studied topic, there have been very few attempts to study beta-diversity over time, especially through seasonal changes. Nevertheless, seasonal change in species composition can become an important management consideration, particularly for migratory taxa such as birds, which occupy northern latitudes only temporarily. In such cases, seasonal beta-diversity needs to be carefully addressed, as it could hamper the representativeness of studies done at a single point in time.

At the scale of the contiguous United States, two major factors should drive variations in seasonal beta-diversity. Across space, broad patterns of bird beta-diversity were best explained by altitude differences within the sampled area, with mountainous regions displaying the highest levels of beta-diversity (Melo et al. 2009). One could thus expect that (1) American states with higher environmental heterogeneity across time (e.g. with major temperature differences between summer and winter months) will exhibit greater bird species composition changes. Many studies have also shown that beta-diversity is dependent on the size of the regional species pool. For example, Kraft et al. (2011) have shown that across latitudinal or elevational gradients, the size of the regional species pool decreases faster than the size of the local communities. This trend results in higher regional over local richness ratios (i.e. beta-diversity) in locations with larger regional species pools, a phenomenon called sampling effects. Transposing to the time dimension, one could expect (2) American states with larger yearly species pools to display higher levels of seasonal beta-diversity because of such effects.

These predictions rely on a broad definition of beta-diversity: changes in species composition between two samples. Recent works have shown that these changes can be partitioned in two additive parts: balanced variations in abundance (species turnover) and abundance gradients (nestedness of the communities), which offer insights into the underlying mechanisms behind differences in beta-diversity (Baselga 2013). This study will thus explore the balance between the two previous forces in shaping bird seasonal beta-diversity across the contiguous US, and see if different beta-diversity components respond differently to these drivers.

METHODS

As the study of seasonal beta-diversity needs data that are both temporally fine-grained and large scale, weekly bird observation frequencies were extracted from the eBird Project (eBird, 2016). Pre-calculated frequency histograms were downloaded for each week and contiguous US state, averaged over the 2006-2016 period. As eBird months are always divided into four weeks, the last week of each month contains between seven and ten days of data. Data retrieval was restricted to an 11-year period to minimize the possible biases due to range changes in times of rapid climate change (e.g. Hitch et al. 2007). Observations were also limited to strict species observations (i.e. hybrids, domestic forms, etc. were removed).

Bird seasonal beta-diversity was assessed by calculating the weekly changes in community composition, based on the pre-calculated species frequencies described above. For each American state, the Horn index of dissimilarity (Horn 1966) was computed for each pair of consecutive weeks (e.g. distance between weeks 1 and 2, distance between weeks 2 and 3, etc.). These numbers were then averaged for a whole year, resulting in one beta-diversity metric per state. Barwell et al. (2015) found that, for species abundance data, the Horn index was the best performing metric (that could be calculated without access to count data) considering a range of desirable properties, including independence of alpha-diversity and absence of bias in cases of undersampling. These properties are especially important here, to both allow the meaningful comparison of beta-diversity between states with alpha-diversity discrepancies and unequal sampling efforts. This method of comparison between weeks at the state scale neglects any competition or spatial structures that might arise in local communities, but is not that far-fetched considering that an eBird checklist is recommended to be anything from a three minutes stationary point count up to a five-mile walk.

To define the hypothesized driving factors, the size of the species pool was calculated as the total number of species reported in a state during the 10-year period. The effect of the temperature differences between summer and winter (from here on the annual temperature range) was defined as the difference between the mean temperature (°C) of the warmest and coldest month in each state. Data for these calculations were extracted from the Worldclim database (Hijmans et al. 2005) at the geographic center of each state on a 10-minute grid, to minimize the effects of highly local phenomena.

To test the relative importance of these two factors, beta-diversity was linearly regressed with both the size of the species pool and the annual temperature range (along with their respective second-order terms) as independent variables. Models with all possible combinations of these terms (9) were ranked based on the small-sample corrected Akaike's information criterion (AICc). Their respective Akaike weights were also calculated, as a measure of relative strength (Burnham and Anderson 2002). The best model from this selection process was inspected for normality and homoscedasticity of the residuals. The contribution of each factor to the explained variance in the best model was assessed through partial regressions (Legendre and Legendre 1998).

Additive beta-diversity components (turnover [BC_{bal}] and nestedness [BC_{gra}]) were calculated as proposed by Baselga (2013). Although these components are based on the Bray-Curtis dissimilarity, they remained relevant in this study, as Bray-Curtis dissimilarity and Horn index were highly correlated (Pearson's r = 0.97). The same modeling steps as above were applied to these two components.

All data analysis was completed with the R software version 3.3.2 (R Core Team 2016).

RESULTS

Regression analysis showed that both the annual temperature range and the size of the species pool are important factors driving bird seasonal beta-diversity, with all three models within the 95% confidence set containing both terms (Table 1). The annual temperature range was related to beta-diversity in a positive accelerating way whereas the species pool size was negatively related (Fig. 1). Both beta-diversity components (turnover and nestedness) displayed similar relationships to the driving factors (Table 2).

Overall, the annual temperature range independently explained 18% of the variation in beta-diversity, the size of the species pool 9% and together (including their shared fraction) they explained 50% of the variation (all adjusted R^2). The resulting distribution of the bird seasonal beta-diversity is thus maximal in north central states where species richness is lower and differences between summer and winter temperatures are larger (Fig. 2).

DISCUSSION

These results suggest that the annual temperature range and the size of the species pool are important factors explaining differences in bird seasonal beta-diversity between American states. The overall map of seasonal beta-diversity (Fig. 2) shows a general increase with latitude, a trend contrary to the one observed in the spatial dimension (Blackburn & Gaston 1996). From a seasonal perspective, it appears that heterogeneity in environmental conditions is more important for bird beta-diversity than productivity or other macro-phenomena decreasing along the latitude gradient. Species temperature affinity or related mechanisms are probably playing a major role here, both (1) positively affecting species turnover, because of a wider range of conditions through the year and (2) negatively affecting the size of the yearly pool, because of patchier sequences of appropriate conditions for each species (White et al. 2006). With the current dataset, it is difficult to assess whether the negative relationship between the species pool size and seasonal beta-diversity is simply correlative (i.e. the annual temperature range drives both phenomena) or if it reveals additional mechanisms. The separate analysis of the turnover and nestedness components of beta-diversity did not provide further insights, as both components reacted similarly to the hypothesized driving factors.

The slope of the beta-diversity—species pool size relationship also suggests that the sampling effects described in Kraft et al. (2011) does not affect bird beta-diversity measurements at the seasonal scale, i.e. the ratio between the weekly and yearly diversity does not change as communities get richer (see Online resource 1).

Although the reported relationships are strong, some caveats are still required. It is well established that eBird data are biased towards urban areas (Sullivan et al. 2009), so the reported results might not be totally representative of the actual seasonal dynamics. This issue could be resolved by using a regular (and finer) grid, although it remains to be seen if the number of samples along the year available at such scales would be sufficient to calculate weekly changes. A finer grid could also detect beta-diversity hotspots associated with migration routes, which are diluted in the current design, and not predicted by this framework.

In conclusion, bird community studies should be interpreted carefully in regions of higher seasonal beta-diversity, as a single snapshot study is less likely to be representative of species composition and interactions in these states.

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Data availability

The dataset generated and analyzed during the current study, along with the necessary computer code, are available in the FigShare repository, https://figshare.com/s/03ff57351ee71a8a3ce7.

Online resources

Online Resource 1. Exploring the gamma:alpha ratio along a latitude gradient (ESM1.pdf)

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TABLES

Table 1. Model selection table for the three best models (95% confidence set), explaining state-scale seasonal beta-diversity across the contiguous United States (n=48). First four columns are model terms and last five are model properties.

Pool size	Pool size^2	Temp. range	Temp. range^2	Df	Log-likelihood	AICc	Delta AICc	Akaike weight
x		x	x	5	209.327	-407.2	0.00	0.633
x	x	x	x	6	209.870	-405.7	1.53	0.294
x		x		4	205.449	-402.0	5.26	0.046

Table 2. Parameter comparison between the best models explaining different components of state-scale seasonal beta-diversity in the contiguous United States (n=48). 95% confidence intervals are provided for each parameter. All variables were scaled before analysis for comparison purposes.

Component	Pool size	Temp. range	Temp. range^2
Total (Horn)	-0.65 – -0.20	0.21 – 0.66	0.05 – 0.30
Turnover (BC_{bal})	-0.63 – -0.09	0.09 – 0.63	-0.03 – 0.27
Nestedness (BC_{gra})	-0.70 – -0.17	0.03 – 0.56	-0.02 – 0.28

FIGURES

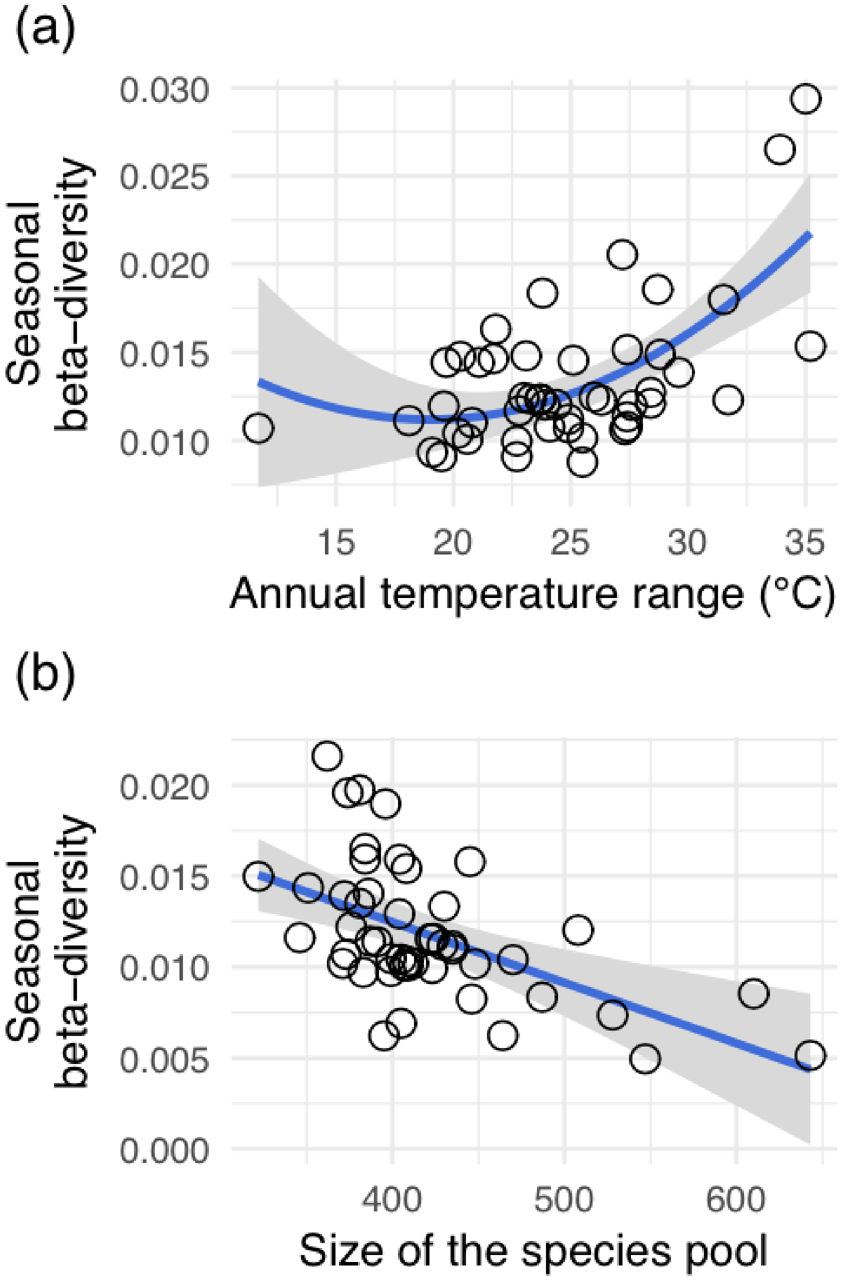

Fig. 1 Relationships between state-scale bird seasonal beta-diversity and hypothesized driving factors. Slope estimates and 95% confidence intervals (blue lines and shaded area) are from the best model, as selected by the AICc criteria. Each point represents a contiguous US state (n=48).

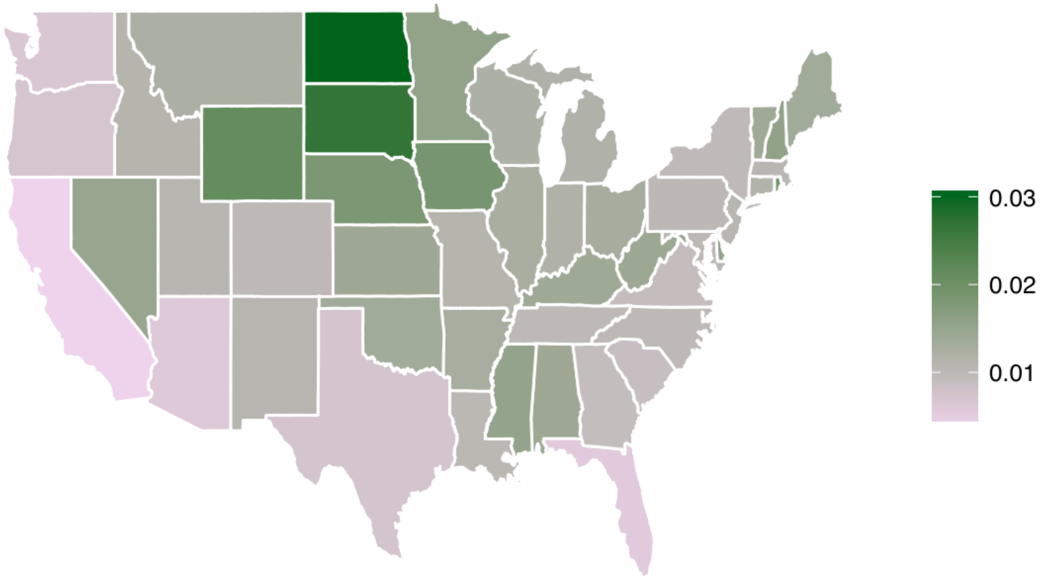

Fig. 2. State-scale bird seasonal beta-diversity, based on eBird weekly frequencies from the 2006-2016 period.

CHAPTER 2

THE ABUNDANCE-RARITY DILEMMA IN CONSERVATION BIOLOGY

Authors : Charles A. Martin , Christopher J Watson, Arthur de Grandpré, Louis Desrochers, Lucas Deschamps, Matteo Giacomazzo, Audréanne Loiselle, Cindy Paquette, Marc Pépino, Vincent Rainville, Raphaël Proulx

Abstract

The rapid changes affecting our planet have two major outcomes on the demographics of living organisms: population decline of common species and extinction of rarest ones. Despite being rooted in similar causes, protecting stocks of abundant species and protecting diversity of the rarest ones requires solutions that are often at odds with one another.

In this study, we demonstrate how rank abundance distribution (RAD) models are mathematical representations of this dilemma. We show that, through their inversion, RAD models can be used to predict species richness, using only the relative abundance of the most abundant species, in 4375 local communities across a range of taxonomic groups.

We found that species richness is predicted without systematic bias when applying a global correction factor. Overall, predictions from the RAD model explained 68% of the variance in species richness, compared to 20% explained by simply regressing species richness on the relative abundance of the most abundant species.

Our results highlight an intrinsic trade-off between dominance and diversity that is present in the structure of RAD models. This dominance-rarity dilemma should remind us that one cannot easily sustain abundant populations of dominant species, say for exploitation, and concurrently maintain species-rich local communities.

Keywords : seasonality; turnover; migration; annual temperature range

INTRODUCTION

Our planet is currently undergoing rapid changes, including global climate modification, large scale habitat conversion, overexploitation of animal populations and unprecedented levels of pollution [1]. All these changes have two major outcomes on the demographics of living organisms: population decline of common species and extinction of rarest ones. For example, the Living Planet Index (LPI) tracks over 16,700 animal populations across the world, many of which are exploited populations. The latest LPI report indicates that demographic indices have declined on average by 60% over the last 50 years [2]. Similarly, Rosenberg et al. [3] estimated that since the 1970s, the North American avifauna has lost over 3 billion birds, which corresponds to a decrease of 29% of its overall abundance, predominantly in abundant species. At the other end of the abundance-rarity spectrum, the IUCN Red List has been developed to monitor global trends in species extinctions, while correcting for the increasing efforts that are deployed in species assessment [4]. Analysis of this list at the global level shows that, in all studied taxonomic groups, the risk of rare species extinction has been constantly increasing since the 1980s [e.g. 5,6]. This rate of species loss is so high that many scientists are now calling the current situation “the sixth mass extinction” [7].

Although both population decline and species extinction are ultimately rooted in similar causes, the range of options available to practitioners differs for each process. It could be that conservation efforts to protect stocks of abundant species are ultimately detrimental to rare species and vice versa [8]. Species invasions are prototypical examples of the influence of abundance on diversity. Recent studies have reported consistent negative effects of plant invasion on the species richness of local communities in plants [9] and arthropods [10]. These syntheses also showed a negative relationship between the extent of species loss and the biomass or cover of invasive plants. Conversely, exploitation of abundant species may have neutral, or even positive, effects on the diversity of local communities if leftover resources become available to rare species. Comparison of species richness inside and outside no-take marine areas revealed a clear positive effect of reserves on fish biomass, but no net effect on algae, invertebrates and fish species richness [11]. The above examples hint at the existence of a dilemma between sustainable stock management and biodiversity maintenance.

The abundance-rarity tradeoff is one of the recurring themes of community ecology, where every community shares a common structure characterized by the presence of few dominant and many rare species [12]. One simple way of representing this structure is to rank species according to their relative abundance in the community (Rank abundance distributions; RADs). Over the years, ecologists have proposed many abundance distribution models [see 12], which range from resource apportionment models (e.g., dominance preemption and MacArthur random fraction) to purely semi-parametric distributions (e.g., log- and geometric-series, lognormal and Zipf-Mandelbrot). Many studies have attempted to identify which models better capture the structure of ecological communities, often with mitigated success [13–15]. Although RAD models are tailored to reflect different ecological processes, their shared mathematical structure can be used to predict community diversity with only minimal information on the most common species [e.g. 16].

The objective of this study is to demonstrate how RAD models suggest the existence of an abundance-rarity dilemma. Specifically, we evaluate whether RAD models can successfully predict species richness (species relative rarity) from the abundance of the most common species (species relative dominance) in thousands of local communities across a range of taxonomic groups. We then discuss the implications of the existence of an abundance-rarity dilemma for management and conservation.

METHODS

Reversing RAD models

RADs can be fitted to observed species abundances, with the underlying parameter values varying freely from one community to the other. In a few cases, the probability of observing a species depends only on the total number of individuals and species richness, as in the case of random apportionment [17] and geometric-series (GS) models. In principle, these simpler models can be inverted to predict species richness from a dominance index. More sophisticated RAD models are less easily inverted as they require the estimation of free parameters, which are obtained by fitting models to the observed data, leading to circular reasoning. For the purpose of this paper, and without loss of generality, our efforts are focussed on the GS model.

The GS model can be described as an iterative process, where each new species arriving in a community takes a given fraction (k) of the remaining resources. The first species thus takes a fraction k of the resources, the second one k(1-k), etc. He & Tang [18] showed that k can be estimated by simply knowing species richness (SR) and the abundances of the least (Nmin) and most (Nmax) abundant species as :

$$k = 1 - \left(\frac{Nmin}{Nmax}\right)^{\frac{1}{SR-1}} \qquad (1)$$

By rearranging Eq. 1 to isolate SR, one can use the maximal relative abundance in a community (MaxRel, which is effectively equal to k +/- an error term) to predict the SR of a community from the abundance of its dominant species and the Nmin/Nmax ratio which, assuming the rarest species was only detected once, is equivalent to 1/(MaxRel*Ntot) :

$$SR = \left[\frac{ln\left(\frac{1}{MaxRel \cdot Ntot}\right)}{ln(1-MaxRel)}\right] + 1 \qquad (2)$$

This formula estimates SR in different communities by only fixing the total number of individuals sampled (Ntot) and the relative abundance of the most abundant species (MaxRel). In species rich communities it is often the case that practitioners can easily identify the most common species.

Dataset preparation

The BioTIME database [19] contains a large collection of ecological communities across the globe aimed at evaluating temporal trends of biodiversity in ecological assemblages. To explore the idea of predicting the species richness of a community through the abundance of its most common species, we downloaded the full BioTIME dataset on December 12 2019, and filtered it to keep only observations from animal communities (see Table 1 for a per taxa breakdown). We excluded plants because Nmax and Ntot are ill-defined when biomass or cover is used as abundance measures. Similarly, we eliminated communities in which Nmin and Nmax were equal (i.e. maximum evenness) because the GS model is not properly defined for these limit cases.

RAD models assume that species interact and share a common set of resources. To prevent the inclusion of communities that are mainly structured by environmental heterogeneity, rather than resource partitioning, we restricted our analyses to studies with a spatial grain less than 1 km^2. We acknowledge that this cutoff grain is still fairly large and that some of the observed variation in species richness could nevertheless be caused by processes other than resource partitioning. We hereby assume that the authors of the original studies identified the proper spatial grain for their target organisms. Finally, we used the most recent data point for each site, resulting in a final dataset of 4375 independent animal communities.

For each community, we calculated the relative abundance of the most abundant species and used it in combination with total abundance to predict SR as per Eq. 2. We hereby adopted an inclusive definition of “local community”, which is a collection of individuals from different species that share (are sampled in) the same area, over the same period, using a common sampling protocol.

Error magnitude and direction assessment

For each community, we calculated the prediction error from the inverted GS model as a log-log residual, i.e. $\log(SR_{observed}) - \log(SR_{gs})$, where $SR_{observed}$ is the species richness tallied in each community and SR_{gs} is the species richness estimated through the inverted GS model.

To assess the magnitude of the prediction error, we calculated the mean absolute error (MAE), and then back-transformed it so that it could be interpreted as an error ratio :

$$MAE = e^{\sum_{j=i}^{n} \frac{|l|}{n}}$$

Where l is the log-log residual for each j community.

An MAE of 1 means perfect predictions while, for example, an MAE of 1.3 means 30% error.

We calculated the direction of errors (i.e. systematic bias) as the mean bias error (MBE), and also back-transformed it to ease the interpretation.

$$MBE = e^{\sum_{j=i}^{n} \frac{l}{n}}$$

The further MBE is from 1, the more biased are the residuals to a particular side. A value of MBE larger than 1 means positive residuals, thus an underestimation of SR. Conversely, MBE values smaller than 1 means negative residuals, thus a systematic overestimation.

Bias correction

The GS model is known to be a steeply-decreasing RAD that underestimates the SR of species-rich communities. To estimate an empirical correction factor (cf) that could reduce this bias, we fitted the following least-square model:

$$log(SR_{observed}) = cf \times log(SR_{gs}) \qquad (3)$$

This model was adjusted using the lm function in R [v 3.6.2; ,20]. Residuals were visually assessed for normality and homoscedasticity.

RESULTS

We predicted the SR of 4375 local communities from around the world using only the abundance of the most common species and the total number of individuals. The relative abundance of the most common species (MaxRel) across all datasets and communities ranged from 0.061 to 0.995, with the median at 0.448. The GS model successfully predicted SR in actual communities, as assessed by the squared correlation between log-predicted and log-observed species richness (pseudo-r^2 = 0.68; Fig. 1a). By comparison, the pseudo-r^2 of the log-log relationship between MaxRel and observed species richness was much lower at 0.20. In other words, inversion of the GS model greatly improved the prediction of species richness in comparison to empirical models using only the MaxRel as the predictor. Although our predictive approach presented a reasonable fit to the observed data, the global error magnitude is nonetheless relatively high with a MAE of 1.66 (i.e. 66%).

As expected from its steeply declining nature, the GS model fit was systematically biased (Fig. 1a). On average, the model underestimated SR (MBE = 1.56), especially for species-rich communities. We found that multiplying log(SR) by a correction factor (cf) of 1.20 (+/- 0.004 SE) both reduced error magnitude (MAE* = 1.45; i.e. 45%) and overall cancelled the systematic bias (MBE* = 1.04) (Fig. 1b, see Table 1 for a per taxa breakdown). This empirical cf was obtained at no extra cost of input variables and can be factored in Eq. 2 directly. However, systematic bias > 30% could still be detected for mammals, as well as for fish and benthos, even after applying the cf.

The general abundance-rarity dilemma is illustrated in Fig. 2. Using a grid of parameter values where *k* ranged from 0.05 to 0.95 and *NTot* ranged from 5 to 100 in Eq. 2, an envelope of possible species richness values for a specific number of individuals clearly emerge : unless the initial number of individuals is very small, increasing the total number of individuals in a community limits the possible species richness values at a site (Fig. 2). The more individuals there are, the less diverse a community can be.

DISCUSSION

We showed that the inversion of simple RAD models can be used to approximate SR with a minimum of information on the relative abundance of the most common species in the community. Because of the steeply declining nature of the GS model, a global correction factor was needed to predict SR without a systematic bias in most communities.. Our results suggest an intrinsic trade-off between dominance and diversity (i.e., the long-tail of locally rare species in RADs), irrespective of taxa or sampling protocol. The generality of the dominance-rarity dilemma should remind us that one cannot easily sustain abundant populations of dominant species, say for exploitation, and concurrently maintain species-rich local communities.

With a 66% error on SR estimates, the non-corrected approach is not particularly well suited for surveying individual animal communities. In a nutshell, the SR of a 20-species community predicted by the GS model could fall anywhere between 8 and 24 species (first and third quartiles for 103 communities of exactly 20 species; Fig. 1a). As hinted above, a large part of this error comes from species rich communities, for which the GS model is not particularly well suited. This is a major limitation of our study, in that, in order to keep the model reversion process tractable, we had to resort to a more rigid RAD model. However, as a simple correction factor effectively decreased bias and restored global symmetry around SR estimates, our conclusions about the existence of a general abundance-rarity tradeoff still hold. Although not as elegant as the inversion of a more flexible model, the corrected GS model still explains more than two thirds of the variance in species richness across thousands of communities, and thus supports the existence of a general abundance-rarity tradeoff. Nevertheless, considerable bias asymmetry persisted for some taxonomic groups like mammals and some aquatic organisms, which would warrant a more in-depth analysis of the individual studies context to further our understanding of the variation in predictive ability among taxonomic groups.

Implications of the abundance-rarity tradeoff would be pervasive, particularly in the management of invasive species and in the sustainable exploitation of natural capital. Release of exploitative pressure on invasive species may induce dominance and cascade negatively on the species richness of local communities [aka enemy-release hypothesis; 21]. Hence, the suppression of abundant (invasive) species should increase diversity by allowing resources to be shared more evenly. The abundance-rarity tradeoff would also impact the exploitation of the natural capital. For instance, halting the harvesting of abundant fish stocks may help restore densities and increase the long-term viability of populations. Intuitively, one might expect that the whole community should benefit from such policies, but our model above (particularly Fig. 2) suggests that, overall, one might see a decrease in species richness in those areas. The abundance-rarity tradeoff could thus explain why some no-catch marine areas do not report evident changes to their species richness compared to exploited communities, despite ongoing habitat alterations outside reserves [11]. This would suggest that, in some instances, we might end up with conservation objectives that cannot be resolved concurrently. Catch-all statements such as “restoring a community” would need much more precise descriptions, because adding individuals to the community could hurt species richness and vice-versa.

The negative dominance-rarity relationship behind all RAD models suggests that conserving both the natural capital of abundant stocks and the diversity of species is a challenging task. Some authors even proposed that RADs are not unique to ecology, but are inherent distributions that emerge in nearly all dynamic systems where a fixed quantity of resources, or "wealth", is apportioned among users [22]. The shared mathematical structure of RAD models could be worded as follows: "It is common to be rare, no matter what". The generality of this maxim has deep implications for the management of ecosystems. It underlines the presence of pervasive inequalities among resource users, which are only reshuffled by changing the environmental context, and thus, the rules of the apportionment game. It reminds us that strategies aiming solely either at exploiting the natural capital, or at conserving species, are doomed to fail. Instead, protection of biodiversity could be promoted by encouraging a broad range of resource exploitation and socio-economical systems, each with its own set of rules.

Data accessibility statement

The data that support the findings of this study are openly available in FigShare at https://figshare.com/s/506f3da3aaf5f91cb1e8.

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FIGURES AND TABLES

Table 1. Corrected mean average error (MAE*), corrected mean bias error (MBE*) with 95% non-parametric bootstrap confidence intervals (from 1000 resampled datasets), number of communities (n) and average species richness (SR) breakdown by taxa. Errors are back-transformed means of log-log residuals of the corrected geometric-series model.

Taxa	*MAE**	*MBE**	n	*SR*
Benthos	1.53 (1.47–1.61)	1.34 (1.26–1.42)	177	30.8
Birds	1.37 (1.35–1.40)	0.82 (0.80–0.85)	546	15.9
Fish	1.55 (1.52–1.58)	1.33 (1.30–1.37)	1168	22.6
Mammals	1.42 (1.39–1.45)	0.77 (0.75–0.79)	626	4.2
Marine invertebrates	1.45 (1.43–1.47)	1.04 (1.02–1.07)	1613	12.7
Terrestrial invertebrates	1.22 (1.20–1.25)	0.98 (0.95–1.02)	231	6.6
Other	1.15 (1.08–1.25)	0.97 (0.87–1.06)	14	3.8

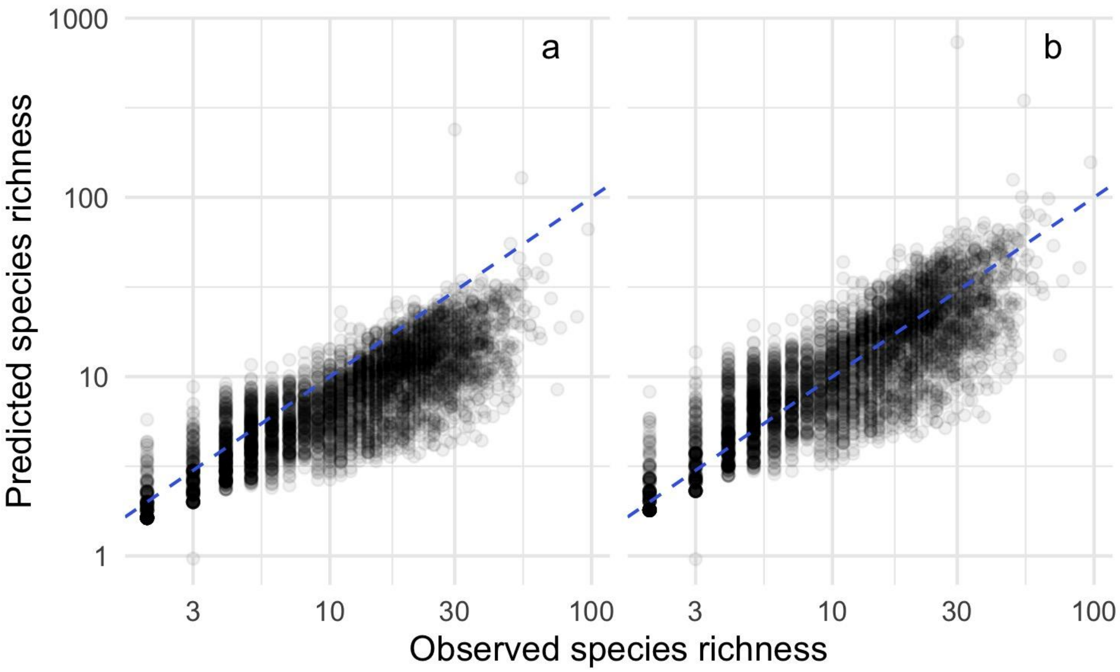

Fig. 1 Relationship between observed species richness in 4375 animal communities and the raw predictions from a geometric-series model (a) and the predicted values after an empirical correction (b). Dashed line is the 1:1 relationship.

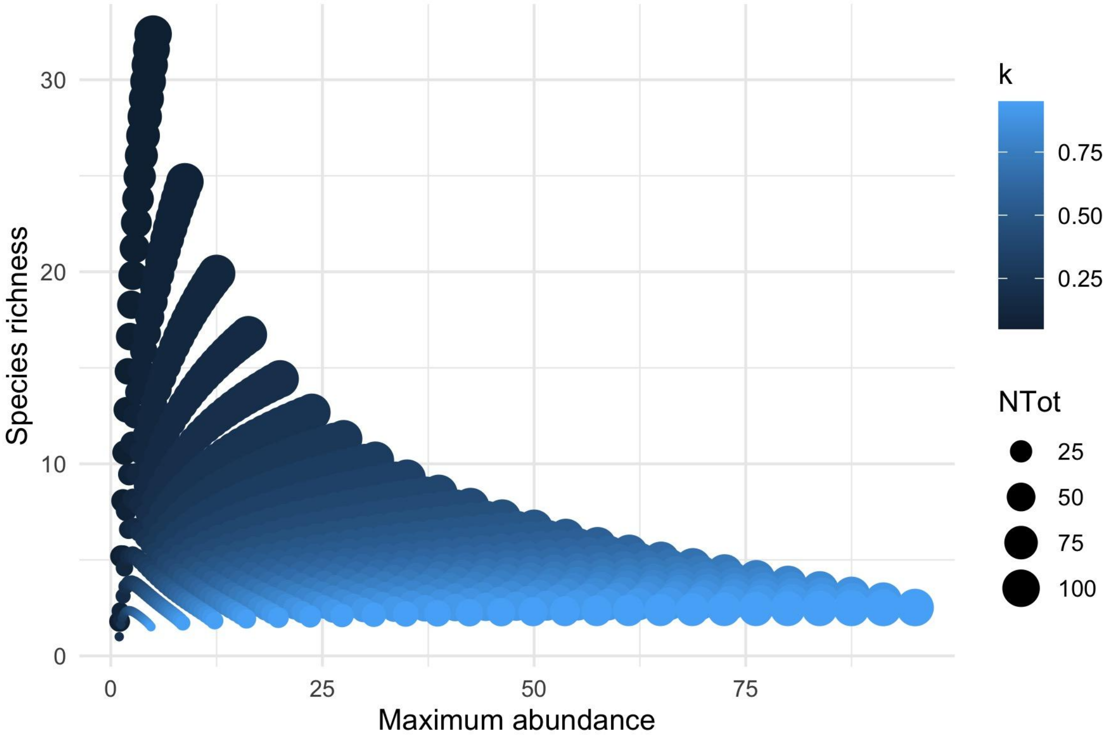

Fig. 2 Theoretical relationship between species richness and total number of individuals in a community, based on Eq. 2.

CHAPTER 3

AN EARLY SYNTHESIS OF THE HABITAT AMOUNT HYPOTHESIS

Author : Charles A. Martin

Landscape Ecology volume 33, pages 1831–1835 (2018)

Abstract

Context The ecological literature is filled with studies highlighting the importance of both habitat loss and fragmentation on biodiversity. The patch concept has been central to these findings, being also at the heart of many ecological theories. Recently, the habitat amount hypothesis has been proposed as an alternative, where the patch concept is put to a rest, and both patch size and patch isolation effects on species richness are reduced to a single gradient: habitat loss in the landscape.

Objectives As this theory stated clear predictions that could be experimentally tested, many formal tests of the hypothesis have been published recently and this study aims at synthesizing their results.

Methods A meta-analysis of 13 tests of the habitat amount hypothesis was conducted, to produce a single combined test of the theory.

Results The 13 tests combined suggest that effects of patch size and isolation, while controlling for habitat amounts, do exist although their overall effect is weak (r = 0.158).

Conclusions Literal interpretations of the habitat amount hypothesis, where patch size and isolation have absolutely no effect on species richness, are probably oversimplifications of the processes at work. Still, the theory could prove useful as a baseline of the effects of habitat loss, against which patch size and isolation effects must be contrasted.

Keywords: habitat amount hypothesis; fragmentation; meta-analysis; biodiversity; species richness

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INTRODUCTION

Limitations in habitat availability are currently the most important threat to global biodiversity (Pimm et al. 1995), and are hypothesized to remain the largest threat in the foreseeable future (Sala et al. 2000). Accordingly, thousands of individual studies have shown the negative effects of habitat loss (Fahrig 2003). As habitat loss is not a homogeneous process, it creates all sorts of patterns in space (i.e. changes in habitat configuration), which ecology also has a long tradition of studying, from Levins' (1969) equilibrium model to the metacommunity concept (Wilson 1992, Leibold et al. 2004). Changes in habitat configuration (e.g. patch size, connectivity, etc.) are also known to have profound effects on ecosystems (Haddad et al. 2015) and we have now come to a point where habitat configuration is integrated into conservation recommendations (e.g. Strobl 1998, Rosenberg et al. 1999) and is part of the reserve selection process (Margules & Pressey 2000, Briers 2002). Conservation being foremost a matter of prioritization, ecologists have long been trying to quantify the relative importance of habitat amounts and configuration for decision-making purposes, with varying results (Didham et al. 2012). The crux of the matter here being that habitat loss necessarily implies changes in configuration, and thus independent effects of either habitat amounts or configuration are often hard to disentangle.

The above conceptual model was strongly challenged when Fahrig (2013) proposed the habitat amount hypothesis (HAH), in which she questions the existence of distinct effects of patch size and isolation on species richness and implies that the effects of such patch-scale configuration metrics could be reduced to a single measure: habitat amount in the landscape. Such a bold statement came with pretty strong arguments (e.g. Fahrig found no evidence that the slopes of species area relationships were different between fragmented and homogeneous landscapes), but also important implications. The most important one being that half a century of research could have been wrongly assigning population processes to patch effects, which could have been as well explained by habitat amounts in the local landscape. The hypothesis was heavily criticized because, among other things, it was described as a phenomenological model that ignored the underlying mechanisms (Hanski 2015, Haddad et al. 2017). Fortunately, the HAH also came with clear predictions to test its claims (but see Haddad et al. 2017 about their independence). The main prediction (and probably the most controversial one) being that, while keeping the amount of habitat constant in the landscape, species richness on a plot, i.e. species density, should not increase with the size of the local patch being studied.

Since Fahrig's article was published, many research teams have tackled the task of testing the habitat amount hypothesis, and this article aims at synthesizing their results, to provide an early idea of where we stand, five years after the publication of the hypothesis.

METHODS

I searched the Scopus database (http://www.scopus.com) on May 29, 2018, for articles explicitly testing the habitat amount hypothesis with the following query: TITLE-ABS-KEY ("habitat amount hypothesis"). From the resulting 15 articles, two were discarded as they were the seminal article and the ensuing discussion (i.e. Fahrig 2013, Fahrig 2015). The remaining texts were carefully examined to ensure they were proper tests of the theory and that they (or their supplementary materials) provided numerical summaries that could be converted to a common effect size. Some studies were thus removed because they were either completed on actual islands or did not provide a metric of patch size or isolation (Rabelo et al. 2017, MacDonald et al. 2018, Piano et al. 2017, De Camargo et al. 2018). Finally, two studies were removed from the dataset because they did not provide parameter estimates or the necessary details to reconstruct them with the published information (Moreira et al. 2017, Pulsford et al. 2017). Multiple tests of the theory in the same article were considered as separate entries, provided that they were not using the same data. In case the same dataset was reanalyzed multiple ways, only the test on the most complete subset was selected. The final dataset thus contained 13 tests of the habitat amount hypothesis, from 7 different articles.

For each test, I extracted either the t-value or F-value of the parameter of interest, along with either the degrees of freedom (df) or sample size (n). As n was needed to calculate the effect size variance (see below) and df were needed to convert the test statistics to a common metric, translation was made between the two (df to n or vice-versa) assuming the number of parameters corresponded to the estimates provided in the results (unless explicitly stated otherwise). In three articles, df might have been overestimated because of the presence of random effects in the models.

In the 7 articles, the habitat amount hypothesis was tested either by assessing the existence of a slope difference between SARs of continuous and fragmented areas or by assessing the existence of independent effects of patch size or patch isolation in a model predicting species richness per sample site while controlling for the amount of habitat. Therefore, a positive relationship between patch size and species richness would produce opposite signs for the same reality, depending on the method used. The signs of the coefficients were thus adjusted so that all positive values indicate a positive effect of patch size or a negative effect of patch isolation on species richness, independent of the habitat amount.

F-values and t-values were converted to a common metric (Pearson's r) using equations provided by Friedman (1982), using the appropriate df for each test. As Pearson's r has some problematic distributional and variance properties when computing meta-analyses, these values were further converted to Fisher's z and its corresponding variance metric (which, in contrary to Pearson's r, is independent of the z-value) using equations provided in Borenstein et al. (2009).

To compute a meta-analytic test of the habitat amount hypothesis, I calculated a weighted effect size, using the inverse of Fisher's z variance as weights in a two-level random effects model. Random intercept terms were included for each test, as well as each article, to account for the hierarchical structure of the dataset. The presence of a publication bias in the reviewed literature was assessed with Egger's regression test for funnel plots (Sterne & Egger 2005). All data analysis was completed with the metafor package (version 2.0-0, Viechtbauer 2010) in R statistical software (version 3.4.3, R Core Team 2017).

RESULTS

Combining the 13 individual tests of the habitat amount hypothesis while accounting for the hierarchical structure of the data produced a combined effect size of 0.159 +/- 0.173 (95% CI) in Fisher's z units (Fig. 2). Egger's test for funnel plot asymmetry suggests that there was no significant publication bias that could have systematically skewed this estimate ($z = 0.6526$, $p = 0.5140$; Fig. 1). This combined effect size translates to a partial correlation between species richness and patch size or isolation of 0.158 while controlling for the amount of habitat in the landscape. Cochran's measure of heterogeneity suggests that there is more variability among tests of the habitat amount hypothesis than expected by random sampling variation ($Q = 38.63$, $df = 12$, $p < 0.0001$).

DISCUSSION

This meta-analytic test of the habitat amount hypothesis thus shows that patch size and isolation effects on species richness do exist, but they are weak (r = 0.158) once habitat amounts in the landscape are accounted for. Overall, this is more or less the same conclusion Fahrig (2003) arrived to 15 years ago in a major literature review, where habitat loss had consistent negative effects on biodiversity while habitat fragmentation per se (i.e. controlling for habitat amount) had weaker and more variable effects. This variation in the directionality of fragmentation effects was recently reassessed and, within studies where a significant effect was observed, fragmentation per se had a positive effect on biodiversity at the landscape scale in a majority of cases (Fahrig 2017), although the present synthesis shows that fragmentation-related features (patch size and isolation), measured on the local patch, have generally neutral or negative effects on its species richness. Many reasons could explain such discrepancy, one of which being that fragmentation at the landscape scale, in addition to any possible negative effect, can also increase heterogeneity (Seiferling et al. 2014), an often cited biodiversity driver (Stein et al. 2014). Mechanisms usually invoked to support the heterogeneity-biodiversity relationship include increases in habitat diversity (i.e. number of niches; Tews et al. 2004) and increases in the number of habitat types available within an organism's home range, which some species require or benefit from (i.e. complementation; Law & Dickman 1998). Such benefits of fragmentation per se cannot be captured when the studied guilds are limited to a single habitat type, as required in the habitat amount hypothesis (e.g. forest interior and forest edge species should not be studied together according to the HAH).

Despite the above-mentioned general conclusions about the direction of fragmentation effects, the high amounts of between-study heterogeneity in the test results also support another common idea in landscape ecology, which is that configuration effects are both context (Andrén 1994, Thompson et al. 2002) and taxa specific (Bender et al. 1998, Prugh et al. 2008). Consequently, the development of further tests of the HAH in additional contexts should be strongly encouraged, as it is likely that each context could provide its own unique answer to the question.

Keeping in mind that this synthesis is based only on a handful of tests, it hints that a literal interpretation of the habitat amount hypothesis, where changes in patch size and isolation have absolutely no effect on species richness when accounting for habitat amount in the landscape, is probably an oversimplification of the actual processes at work and misses important context-specific issues. Just like when Hubbell's (2001) unified neutral theory of biodiversity reversed the burden of proof on ecologists to show environmental effects on community structure against a background of neutral processes, Fahrig's habitat amount hypothesis should probably be viewed as a baseline of habitat loss effects, above which habitat configuration effects must be contrasted to be considered as important.

The dataset generated and analyzed during the current study along with related computer code are available in the FigShare repository, https://figshare.com/s/45649772e9cd166b293d.

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FIGURES

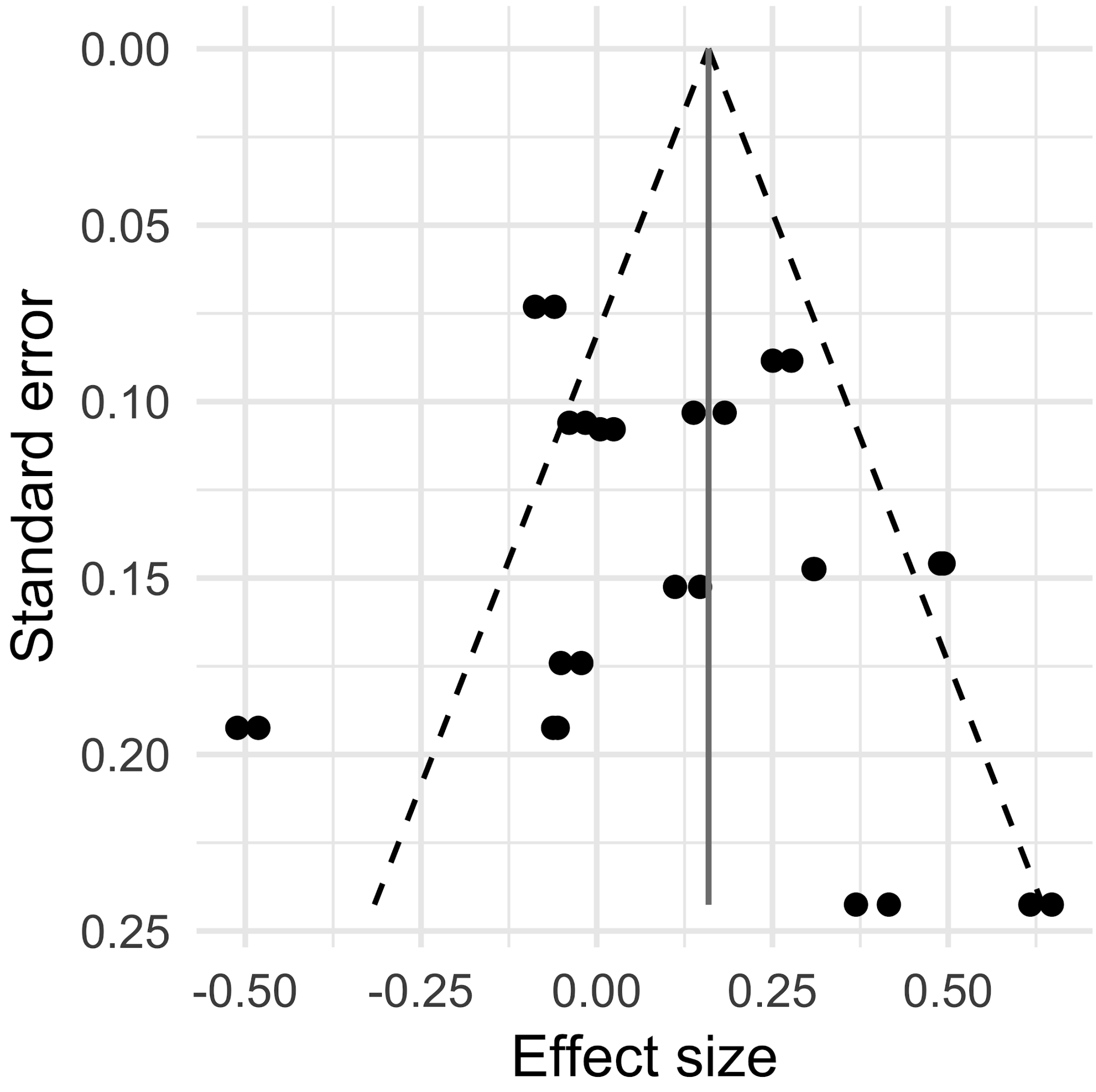

Fig. 1 Visual assessment of the publication bias in tests of the habitat amount hypothesis. Funnel represents the 95% confidence interval. Effect size is Fisher's z.

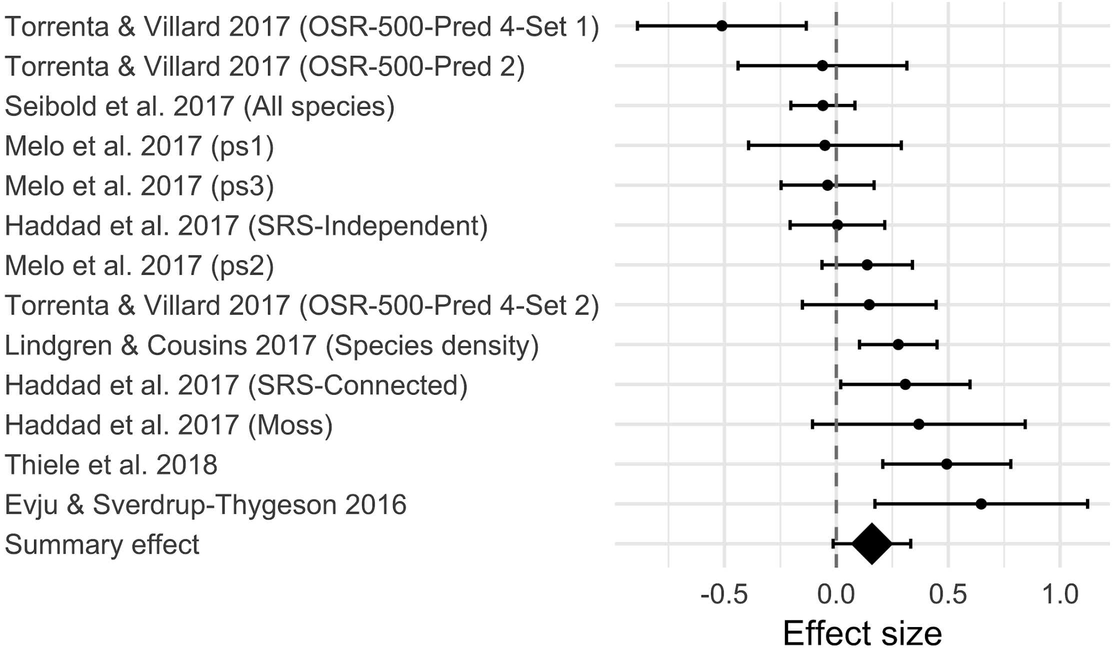

Fig. 2 Meta-analysis of the independent effect of habitat configuration on species richness, while controlling for the habitat amount in the landscape. Effect size is Fisher's z. Each row represents an individual test of the hypothesis and the last row is the summary effect. Error bars are 95% confidence intervals.

CHAPTER 4

HOW THE RELATIONSHIP BETWEEN VEGETATION COVER AND LAND-COVER VARIANCE CONSTRAINS BIODIVERSITY IN A HUMAN DOMINATED WORLD

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Abstract

Context: Alteration of natural vegetation cover across the landscape drives biodiversity changes. Although several studies have explored the relationships between vegetation cover and species richness, as well as between land-cover variance and species richness, few have considered the non-independence of these two biodiversity drivers.

Objectives: The goal of this perspective paper is to present theoretical and empirical relationships linking vegetation cover to land-cover variance at the landscape scale, and the implication of these relationships for species richness change along a gradient of increasing anthropization.

Methods and results: We used simulated and empirical Normalized Difference Vegetation Index data to examine the generality of the relationship between vegetation cover and land-cover variance. Using the province of Québec (Canada) as a case study, our results show that decreasing vegetation cover captures the transition from landscapes with low land-cover variance (non-anthropized landscapes), to intermediate variance (agricultural landscapes), to high variance (urban landscapes).

Conclusion: Based on this relationship between vegetation cover and land-cover variance, and assuming independent positive monotonic relationships between biodiversity and both of these drivers, we predict a unimodal relationship between species richness and anthropization. This suggests a threshold of anthropization beyond which the positive effects of land-cover variance no longer compensate for the negative effects of vegetation cover loss. Identifying these thresholds could be key to setting conservation targets at a landscape scale.

Keywords : biodiversity, conservation, land-cover variance, species richness, vegetation cover, environmental heterogeneity, landscape composition, landscape structure

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INTRODUCTION

A central goal of conservation ecology is to understand how organisms respond to our increasing human footprint. Organisms' responses to habitat alteration are highly complex, multifaceted, and variable among species and across contexts (Bender et al. 1998; Debinski and Holt 2000; Connor et al. 2000; Prugh et al. 2008). Nevertheless, at a landscape scale, the net effect of anthropization is driven in large part by the response of species to changes in vegetation cover and/or changes in spatial land-cover variance. Early conceptual models in landscape ecology expressed the anthropization gradient as follows (Forman 1995; McIntyre and Hobbs 1999): 1) start with a uniform natural landscape with relatively high vegetation cover and low land-cover variance; 2) progress to a heterogeneous semi-natural landscape with an intermediate vegetation cover and increased land-cover variance; 3) end with an impacted landscape with relatively low vegetation cover and low land-cover variance. This trajectory suggests a decreasing relationship between the anthropization gradient (i.e., transitioning from stages 1 to 3 above) and vegetation cover, and a hump-shaped relationship between the anthropization gradient and land-cover variance.

We define vegetation cover as the average leaf area per unit of land area, typically known as the Leaf Area Index. Vegetation cover changes over space in relation to the proportion of land occupied by plants, but also how tall or densely packed plants are. In practice, vegetation cover can be quantified using surrogate measures like the normalized difference vegetation index (NDVI) or the enhanced vegetation index (EVI). Mean vegetation cover decreases along an anthropization gradient if newly created land-cover patches, such as roads, abandoned fields, or crops, do not contain as much leaf area as the original vegetation. Likewise, we define land-cover variance as the magnitude of contrast (in terms of vegetation cover) among different areas within the landscape. Land-cover variance thus measures only compositional heterogeneity, and ignores its configurational component (sensu Fahrig et al. 2011). For present purposes, we quantified vegetation cover as the mean of NDVI values across a landscape and land-cover variance as the mathematical variance of these NDVI values.

Although vegetation cover and land-cover variance are well-studied variables, few authors have investigated how the two are interrelated. We expect they are related, as this is often the case for the mean and variance of measured variables (here, NDVI) (e.g., Tokeshi, 1995). Possible relations for vegetation cover and land-cover variance have been postulated in conceptual models (Tilman and Pacala 1993; Abrams 1995), but the relationship between them remains unexplored. In this perspective paper, we present both theoretical and empirical arguments for the presence of a non-linear hump-shaped relationship between vegetation cover and land-cover variance at landscape scales. We discuss the ecological and conservation implications of this relationship, providing a new perspective on productivity-biodiversity and heterogeneity-biodiversity relationships observed in nature.

How are vegetation cover and land-cover variance related?

A MATHEMATICAL EXAMPLE

Let us imagine a landscape in which vegetation cover is measured on a continuous scale, for example, as NDVI on the bounded interval [-1,1]. Each portion (pixel) of the landscape has a value of NDVI. Let us now assume that the distribution of vegetation cover values over the landscape is described statistically by the Beta distribution:

$$P(x) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\,\Gamma(\beta)}\,(1 - x)^{\beta-1} x^{\alpha-1},$$

which is often the case for ecological variables with bounded distributions (Stoy et al. 2009). Following our definitions of vegetation cover and land-cover variance, the mean is directly related to the α and β parameters of the Beta distribution as follows:

$$E[X] = \frac{\alpha}{\alpha+\beta},$$

and its variance depends on the same two parameters:

$$var[X] = \frac{\alpha\,\beta}{(\alpha+\beta)^2\,(\alpha+\beta+1)}$$

Hence, the mean vegetation cover of a landscape will directly affect the land-cover variance that can be observed (Remmel 2009). The intuition behind such mathematical statements is that, in the context of a bounded distribution, large deviations around the mean can only exist when the mean is towards the middle of the range of possible values. Any distribution with a mean near the upper or lower bound of the range implies small deviations around that mean. This relationship can be visualized by sampling evenly spaced intervals of α and β parameters and calculating the mean and variance of each combination. Technically, the procedure is equivalent to simulating landscapes over a large range of NDVI spatial patterns and calculating the mean and variance of these values. Plotting the mean vs. variance of NDVI values in these landscapes reveals a clear hump-shaped envelope between them (Fig. 1A). Each combination of mean and variance in Fig. 1A translates into a different type of landscape pattern.

EMPIRICAL ILLUSTRATION

To characterize the predicted mean-variance relationship in real landscapes, we calculated vegetation cover and land-cover variance using Sentinel-2 radiometric data (Drusch et al. 2012). We selected 10 000 random longitude and latitude coordinates from a gaussian distribution centered around Montréal, QC (Latitude 45.50, Longitude -73.56, standard deviation 2.5 degrees) covering the whole gradient of ecosystems found throughout the province of Québec (Canada), including tundra, boreal, mixed, and deciduous forests, as well as urban and agricultural areas. A land-cover classification conducted using 2015 data from the Operational Land Imager (OLI) Landsat sensor (Government of Canada et al. 2019) was associated with each pair of coordinates. We removed coordinates falling outside the boundaries of Québec or directly on water, ice, snow or wetland land-cover categories, leaving 8 970 landscapes.

Gradients in vegetation cover and land-cover variance in this dataset stem from a combination of natural (e.g., across biomes) and anthropized areas. For each pair of coordinates, we used Google Earth Engine (Gorelick et al. 2017) to create circular 100 m radius and 564 m radius (i.e., 1 km^2) landscapes centred on the coordinates on Sentinel-2 images (10 m ground resolution). These sizes correspond respectively to the radius around which bird songs can typically be heard in point count surveys and the home range size of most passerine birds (Brown and Sullivan 2005). We refer to these arbitrarily-selected scales as small and large landscapes hereafter. We selected all Sentinel-2 images taken between 1 Jun and 1 Sep 2018, to ensure that they are representative of summertime vegetation cover. For each band and each pixel forming the image, we calculated the median value of the time series to remove the influence of cloud cover and cloud shadows (Namikawa 2017). We then calculated the Normalized Difference Vegetation Index (NDVI; Rouse Jr et al. 1974) for each pixel, using bands B8 (near infrared) and B4 (red). In a subsequent step, we extracted NDVI mean and variance across pixels, which we interpreted as vegetation cover and land-cover variance values for each landscape. Graphically representing these variables together revealed a hump shape, which we illustrated using a thin-plate spline with penalized regression coefficients (Wood 2003). Spline functions fitted to small (100 m radius) and large landscapes (564 m radius) explained respectively 28 and 41% of land-cover variance using only vegetation cover as the explanatory variable (Fig. 1B and 1C).

The vegetation cover gradient captures the transition from natural landscapes with a high vegetation cover (low land-cover variance), to croplands (moderate variance), to urban lands (high variance), and finally to landscapes with a naturally low vegetation cover (low variance) (Fig. 1). In particular, several urban landscapes in southern Québec show very high levels of land-cover variance; i.e., black points in the upper left of the envelope (Fig. 1B and 1C). Considering the proximity of these landscapes to the upper boundary of the relationship, further losses of vegetation cover are likely to translate into decreasing land-cover variance. In other words, the land-cover variance of urban landscapes at the boundary will start decreasing if they are pushed farther to the left on the vegetation cover axis (Fig. 1A).

The extent of the landscape influences some aspects of the cover-variance relationship. Although the overall shape of the data envelope did not change, the strength of the relationship increased with increasing spatial extent. Indeed, at a large spatial extent it is harder to find landscapes with either very high or very low land-cover variance, thus decreasing the deviation range of observed values on that axis. Spatial extent also has implications on the relative position of landscapes along the vegetation cover axis. For instance, the same urban area could reveal a low vegetation cover at a small spatial extent (e.g., a parking lot), but a much higher vegetation cover if observed at a larger extent that incorporates green spaces such as residential yards or municipal parks. The effect of extent will be, especially marked if the landscape overlays different land-cover classifications (e.g., urban and cropland areas).

IMPLICATIONS FOR BIODIVERSITY CONSERVATION

The relationships between vegetation cover and land-cover variance described above have implications for our understanding of how species richness changes along an anthropization gradient. To highlight these implications, let us consider circumstances where species richness increases monotonically with both vegetation cover and land-cover variance. Such a scenario is supported by an extensive literature on the productivity-species diversity hypothesis (Cusens et al. 2012; Gillman et al. 2015) and the heterogeneity-species diversity hypothesis (Tews et al. 2004; Stein et al. 2014). The above hypotheses are represented by positive monotonic relationships between vegetation cover and species richness, as well as between land-cover variance (i.e., spatial heterogeneity) and species richness (Fig. 2).

Conceptually, the anthropization gradient captures how landscapes change as they move along the non-linear relationship between vegetation cover and land-cover variance, and combines their joint effects. These gradients are represented by a decreasing relationship between anthropization and vegetation cover, and a hump-shaped relationship between anthropization and land-cover variance (Fig. 2). Assuming for our purposes that vegetation cover and land-cover variance have independent and additive effects on the species richness of a landscape, a concave relationship is then obtained between species richness and the level of anthropization (Fig. 2).

From our investigation, we speculate that confusion may arise when studying the bivariate empirical relationship between biodiversity variables and vegetation cover at the landscape scale. Although many species might respond monotonically to vegetation cover (Gilroy et al. 2014), our results above reveal that vegetation cover and land-cover variance are in fact interrelated in a non-linear fashion (Fig. 1). Thus, the observed bivariate relationship between vegetation cover and species richness could appear hump-shaped; although this would be the net result of the two factors acting at one on species richness (see Evans et al. 2005).

Our conceptual model predicts a concave response of species richness to anthropization whenever vegetation cover and land-cover variance are respectively a monotonic decreasing and a unimodal function of landscape anthropization. Other studies support the idea that species richness varies unimodally with anthropization. The PREDICTS project, for Projecting Responses of Ecological Diversity In Changing Terrestrial Systems, is a large concerted effort to better understand the influence of land-use change on species richness and composition. The database consists of 320,924 records at 11,525 sites, from 284 publications, including 26,953 species from 13 terrestrial biomes (Newbold et al. 2015). The main results of PREDICTS show that intensive land-use of plantation, cropland, or urbanization is associated with a steep decline of species richness based on rarefied estimates (ca. -40%). In contrast, areas of lower human population density, as well as extensive land cover of primary and secondary natural vegetation, are associated with a slight increase in species richness (ca. +5%). While there exists considerable spatial variation in the data, the overall inference would be that species richness should increase, on average, with increasing human population from low to moderate density (up to 20-40 persons/km^2), then decrease steadily at higher human density (Newbold et al. 2015). In particular, the relationship between species richness and human population density (Extended data Figure 2 in Newbold et al. 2015) bears striking similarities with the conceptual ones presented herein (Fig. 3).

Another global analysis of 375 studies distributed worldwide evaluated the effect of land-use intensity on plant diversity (Gerstner et al. 2014). The study found negative effects of intensive land-use practices, like nutrient-input farming and tree plantations, on plant diversity (correlation of ca. -0.46). Yet, the study also reports positive, although weak, effects on plant diversity of extensive management practices, such as mowing/grazing of grasslands and logging/thinning of forests (correlation of ca. +0.14). Remarkably, abandonment of extensively managed landscapes (e.g., meadow or pasture) decreased plant diversity, while abandonment of intensively managed landscapes (e.g., conventional farming or tree plantation) increased diversity (Gerstner et al. 2014).

We emphasize that the relationship we describe here is not equivalent to other conceptual models that have predicted a hump-shaped response of species richness to increasing temporal disturbance (the intermediate disturbance hypothesis; Connell, 1978) or more recently to spatial heterogeneity; i.e. the intermediate heterogeneity hypothesis (Fahrig et al. 2011) also called the area-heterogeneity trade-off (Allouche et al. 2012). While the intermediate disturbance hypothesis was criticized on both empirical and theoretical grounds (see Fox 2013), the area-heterogeneity trade-off has received some support (Yang et al. 2015, Shuler et al. 2017, but see Ben-Hur and Kadmon 2020). These two hypotheses suggest that "environmental variation", either in time or space, drives species coexistence. In contrast, we herein propose that this environmental variation is a (non-linear) function of vegetation cover change, and that both factors affect species richness at the landscape scale. We also note that our framework has the advantage of clearly defining landscape properties in terms of mean and variance of the vegetation cover. This last point is particularly important as concepts like "disturbance" or "heterogeneity" have received multiple interpretations in the literature (e.g., Stein and Kreft 2015). Even the term "area" in the area-heterogeneity trade-off can be challenging in practice because it implies that species habitats are discrete, measurable quantities. However, the generality of the framework we propose also has its downsides, as it makes no prediction about which species should be favoured or disfavoured with increasing anthropization. For example, species richness may increase mostly through the addition of cosmopolitan exotic species as well as a few disturbance-tolerant native species (McKinney and Lockwood 1999, McCune and Vellend 2013).

FUTURE DIRECTIONS

In a metapopulation-based model describing species coexistence in patches of fragmented habitats, Tilman et al. (1994) showed that the relationship between the proportion of habitat destroyed and the proportion of species driven extinct should be relatively flat in the early stages of anthropization and rapidly accelerate with further habitat loss. Syntheses of biodiversity changes at landscape scales in the Anthropocene point to a flat response, or even a slight increase with anthropization of species richness in plants (Vellend et al. 2017) and vertebrates (Pautasso 2007). Such compensatory effects could precede the steeper and more consequential part of Tilman et al.'s (1994) prediction, where species extirpation rapidly increases following further habitat losses. However, Tilman's model assumes that no species can survive in habitats with a vegetation cover below some level. The conceptual model we propose here offers a simple, yet realistic, explanation for the observed increase in biodiversity with landscape anthropization. Increasing land-cover variance in the early stages of anthropization might compensate for natural habitat loss (Fig. 1). It suggests that each landscape has a threshold beyond which the loss of vegetation cover will switch from increasing to decreasing variance, with synergistic negative effects on the persistence of species. Identifying where this shift occurs along various anthropization gradients and environmental contexts could be key in setting conservation targets at a landscape scale. Future work on this topic should explore the influence of spatial scale (Fig. 1), as well as assumptions of a linear mapping of species richness on vegetation cover and land-cover variance (Fig. 2).

In summary, our framework implies that species richness responses to land-use intensification result from the opposing effects of decreasing vegetation cover and increasing land-cover variance at low to moderate anthropization levels, and from synergistic negative effects of these two factors at high anthropization levels. Results from two global syntheses so far corroborate these general predictions across many species and environmental contexts (Gerstner et al. 2014; Newbold et al. 2015).

DECLARATIONS

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Code availability: The code is available on Figshare: 10.6084/m9.figshare.12937241

Authors' contributions: All authors contributed to the writing and conceptual framing of the paper. CM and RP conceived and managed the study. CM compiled the data, conducted analyses and made the figures.

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FIGURES

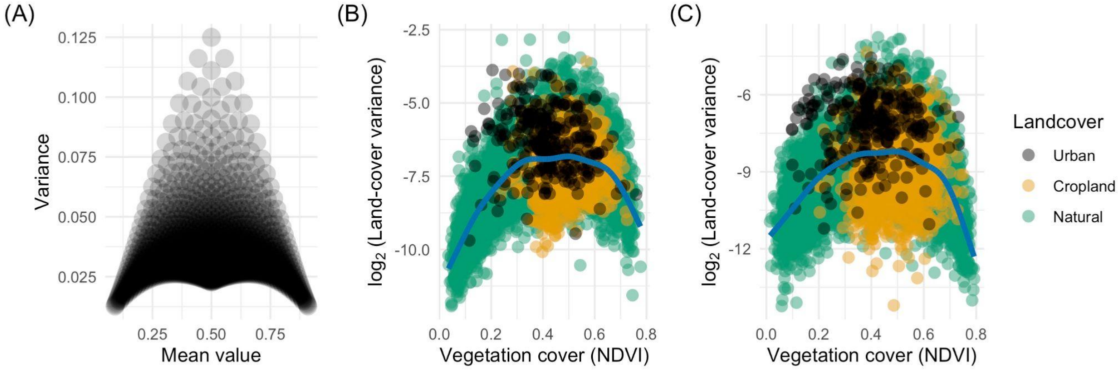

Fig. 1 Mathematical and empirical relationship between vegetation cover and land-cover variance. Each point on a plot represents a prediction (A) or observation (B and C) for an individual landscape. (A) Predicted relationship between vegetation cover and land-cover variance based on the mathematical parameterization of a Beta distribution. Each pair of mean and variance values notionally represents the mean and variance of vegetation cover for a hypothetical landscape. They are sampled from the Beta distribution, using an evenly spaced grid of α and β parameters, both ranging from 0.5 to 5.0. (B and C) Measured relationship between vegetation cover and land-cover variance measured in 8970 landscapes across the province of Quebec, Canada, at two different scales (B: 564-m-radius landscapes, C: 100-m-radius landscapes) with corresponding land-use category. Vegetation cover and land use variance were calculated for NDVI values across each landscape. Land-cover variance was log-2 transformed to better visualize the hump-shaped pattern.

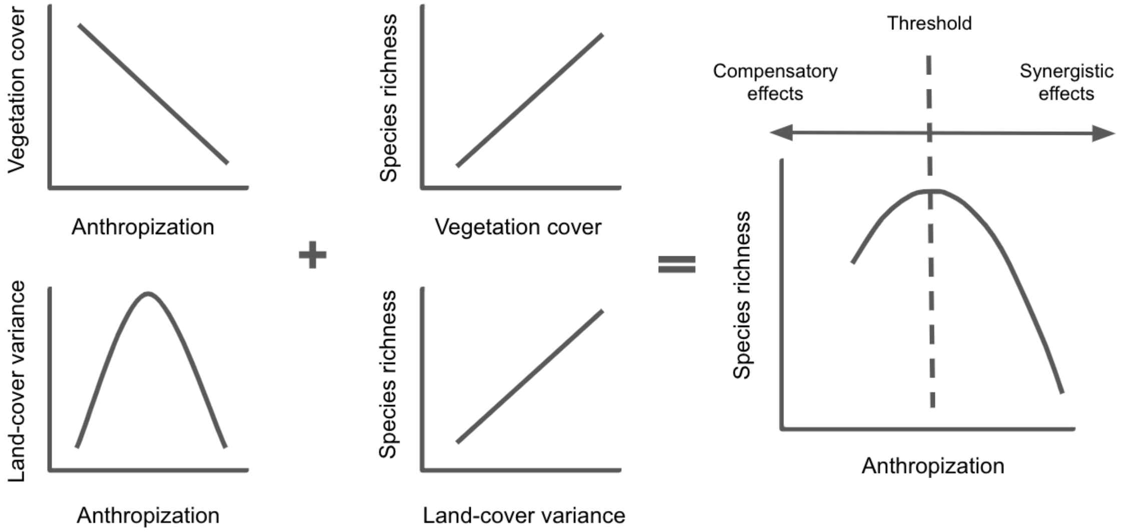

Fig. 2. Conceptual representation of the net effect of vegetation cover and land-cover variance on species richness along the anthropization gradient. The framework assumes positive monotonous relationships between vegetation cover and species richness, as well as between land-cover variance (i.e., spatial heterogeneity) and species richness. Conceptually, the anthropization gradient captures how landscapes change as they move along the non-linear relationship between vegetation cover and land-cover variance, and combines their joint effects. These gradients are represented by a decreasing relationship between anthropization and vegetation cover, and a hump-shaped relationship between anthropization and land-cover variance. Assuming that vegetation cover and land-cover variance have independent and additive effects on the species richness of a landscape, a concave relationship is obtained between species richness and the level of anthropization.

CHAPTER 5
DISTAL VS. PROXIMAL DRIVERS OF FOREST BIRD SPECIES RICHNESS

Authors : Charles A. Martin & Raphaël Proulx

Abstract

Aim
Two main theories usually explain natural gradients in species richness : the productivity-diversity theory and the heterogeneity-diversity theory. But despite important potential implications, the existence and the shape of a constraining relationship between productivity and heterogeneity has rarely been discussed in diversity studies. We aim to explore this relationship and its implications on the study and conservation of species richness.

Location
Our study was performed in 87 forested patches in 5 temperate landscapes in the province of Québec, Canada, including both protected and unprotected areas.

Time period
Summer of 2015

Major taxa studied
Songbirds and woodpeckers.

Methods
As both productivity and heterogeneity have many different definitions and measurements, we quantified both measures from a vertical (i.e. space filling) and an horizontal (e.g. land cover) point of view, using respectively *in-situ* photography and remote sensing data. These measurements were then related

in a causal model to forest bird species richness from point count data. In this initial model, horizontal productivity was hypothesized as the driver behind both horizontal heterogeneity and vertical productivity, whereas vertical heterogeneity was driven solely by vertical productivity and the four variables were driving bird species richness.

Results

Once accounting for the probable dependency structure between heterogeneity and productivity components, the only driver to which birds seem to directly respond (the proximal cause) was horizontal heterogeneity. The final conceptual model shows that the main driver behind productivity and heterogeneity variables is horizontal productivity, and because of its strong and constrained relationship with horizontal heterogeneity, horizontal productivity can be considered the ultimate driver of bird species richness.

Main conclusions

From a conservation perspective, our results mean that once we've correctly parameterized the productivity-heterogeneity relationship, we could measure a single variable and infer the value of the other, going back to a bivariate model. This would simplify greatly the construction and interpretation of species richness models. On the other hand, it means that in any particular site where the landscape was artificially moved away from the typical productivity-heterogeneity relationship (e.g. by human interventions), assessment using only a single metric could be misleading and strongly needs to be avoided.

Keywords : productivity, heterogeneity, species richness, forested landscapes, bird conservation

INTRODUCTION

Understanding variations in species richness has been one of the long standing goals of ecology. In addition to the conceptual appeal of grasping why things vary in nature, understanding variation in species richness also has some serious conservation implications. From a prevention point of view, understanding what are the contemporary drivers of species richness is critical to guide our actions, in order to preserve as much species diversity as possible. Furthermore, a solid understanding of species richness drivers would also allow us to predictably restore species richness in areas where it might have regressed because of human interventions.

Of the many factors affecting species richness, one of the most ubiquitous is its relationship with productivity. Richness-productivity relationships have been observed for about every possible taxa including plants (Adler et al., 2011), birds (Koh et al., 2006), butterflies (Kerr, 2001) and benthic animals (Chase & Leibold, 2002). These patterns have also been deduced many times from theoretical models (Wright, 1983; Kondoh, 2001). Productivity, as used herein, is a catchall term, encompassing many different concepts, from very specific measurements such as NDVI (Koh et al., 2006), standing crop (Al-Mufti et al., 1977) and potential evapotranspiration (Currie, 1991) to vaguer definitions such as available energy (Wright, 1983) and large scale proxies like latitude (Gillman et al., 2015). Although incredibly common, richness-productivity relationships come in many shapes including positive linear, negative linear and unimodal (Waide et al., 1999; Mittelbach et al., 2001). As of now, there does not seem to exist a single canonical shape (Mittelbach et al., 2001; Whittaker, 2010; Šímová et al., 2013), many authors hypothesizing that the observed shape is scale dependent (Currie, 1991; Waide et al., 1999; Chase & Leibold, 2002; Whittaker, 2010; Gillman et al., 2015).

A second important and highly studied pattern of species richness is its variation with environmental heterogeneity. Richness-heterogeneity relationships have been observed for a variety of taxa, from invertebrates to mammals and herptiles (Tews et al., 2004; Stein et al., 2014). In the last decade, they have been particularly well studied in birds (Koh et al., 2006; Allouche et al., 2012) and plants (Parviainen et al., 2010; Tamme et al., 2010). Despite its pervasive use in ecology, environmental heterogeneity is seldom defined, and its applied measurements are often defined on a per-study basis. Nevertheless, two broad types of heterogeneity are usually related to species richness. One classical way to study richness-heterogeneity relationships is from a vegetation structure point of view, where having more layers of vegetation (or a more varied structure) is deemed more heterogeneous (MacArthur & MacArthur, 1961). A second common way to study environmental heterogeneity is through the number of (or variation in) habitat types within a landscape (Roth, 1976). Although both definitions are effectively measuring heterogeneity, it is easy to realize that they represent completely different realities (or scales) from an organism's perspective. For sake of brevity, we'll refer to these respectively as vertical and horizontal heterogeneity. With such a wide gamut of definitions, one should not be surprised that the measured relationship between species richness and heterogeneity also takes on many different shapes (linear positive, linear negative, hump shaped, etc.) and that many authors have previously realized it is also a scale-dependent phenomenon (Tews et al., 2004; Tamme et al., 2010; Stein et al., 2014).

For both above relationships (richness-heterogeneity and richness-productivity), feedback mechanisms have been observed when both species richness and heterogeneity/productivity are evaluated at the same trophic level. For example, there are studies showing that plant species richness can increase productivity through mechanisms such as functional complementarity and functional selection (Cardinale et al., 2007), whereas other studies have found that plant species richness is itself driven by productivity (Mittelbach et al., 2001). Herein, we'll limit our discussion to the simpler case where productivity and heterogeneity are measured at one trophic level, and species richness is measured on a second level, which uses the first one as a resource, conforming more or less to classical niche theory models.

Despite important potential implications, the existence and the shape of a constraining relationship between productivity and heterogeneity has rarely been discussed in species richness studies. It has recently been suggested that, both mathematically and empirically, the relationship should be strongly constrained and non-linear, which would mean that bivariate relationships with species richness could have been highly misleading (Martin et al., submitted.).

Knowing all of the above, the present study will thus explore the empirical relationship between productivity and heterogeneity and its implication on the study and conservation of species richness. We will do so using both the vertical and horizontal dimensions of heterogeneity and productivity. Patterns of bird species richness in forested environments will be our focus, as birds have previously responded rather clearly to both dimensions of heterogeneity, as well as being a highly studied and emblematic model organism. Our study reveals that, for forest birds, the proximal driver of species richness is horizontal heterogeneity, but that ultimately, it is controlled by horizontal productivity through a highly constrained heterogeneity-productivity relationship.

METHODS

Study areas

Sites for this study were selected in five separate areas in Québec (Canada), sampling a wide variety of forested environments from temperate climates (Table 1). Some of these areas were located in protected zones (Bic, La Mauricie and Sutton) while one was, at the time of the measurements, in a planned protected area (Abitibi), whereas sites in Chibougamau had no protection status. In each of the five areas, 20 sites were initially selected, at least 500 m apart from each other, to cover as much of the available habitat gradient as possible in the selected area.

Horizontal measurements

Horizontal productivity and heterogeneity variables were prepared in a two step process, using Sentinel-2 radiometric data (Drusch et al., 2012). For each study area, a polygon was created around the whole area with Google Earth Engine API, and any Sentinel-2 image overlapping the polygon (as of November 30th, 2018) was extracted at a 10 m resolution. These images were then filtered to keep only those obtained yearly between June 1st and September 30th, to ensure that they are representative of summer-time productivity. For each band forming the image, the median value was then calculated to crudely remove any potential extreme values due to cloud cover (Namikawa, 2017). Normalized difference vegetation index (NDVI; Rouse Jr et al., 1974) was then calculated for each pixel, using information bands B8 and B4. Each of these NDVI buffers were then saved as TIF files and stored locally. In a subsequent step, NDVI mean and variance were calculated for each site inside an 85 m buffer with the raster package version 2.8-19 (Hijmans, 2019) in R version 3.5.1 (R Core Team, 2018). This 85 m radius corresponds roughly to the area censused by the bird recordings at each site (unpublished data). These mean and variance values are interpreted hereafter as horizontally measured productivity and heterogeneity.

Vertical measurements

To find a ground-based equivalent to the pixel-based approach of the horizontal method described above, an in-situ photographic protocol was established. With a DSLR camera (Canon EOS REBEL T5i; Canon Inc., Tokyo, Japan), high-resolution JPEG pictures were taken horizontally and at a 45° angle (i.e. looking up at the canopy) in every cardinal direction, for a total of 8 pictures per site. All pixels forming an image were then averaged to a single RGB triplet, and were treated like a single pixel for image analysis purposes. The green chromatic coordinate (G / [R + G + B]; Gcc; Sonnentag et al. 2012) of each image was then calculated. The mean of all 8 Gcc values at a site was used as a measure of vertical productivity and the variance as a proxy for the vertical heterogeneity present in each site.

Bird species richness

To assess bird species richness, a rainless morning with relatively low winds was selected in June or early July in each area to make continuous recordings of the bird communities, from sunrise to 9 AM (Regroupement Québec Oiseaux et al., 2011) with a digital sound recorder (H2n Handy Recorder; Zoom, Tokyo, Japan) at all sites for an area simultaneously. For various reasons (batteries draining out too rapidly, recorders not properly started before leaving the site, etc.), not all recorders sampled the complete morning up to 9 AM. As such, only 87 sites have enough recording time to be analysed hereafter (see Table 1 for details about sample size in each area).

For each site, every songbird or woodpecker species was identified in five 3-minute samples from 6 AM to 9 AM. The total number of species identified in each site (i.e. gamma diversity) was then used as a measure of bird species richness, and varied between 5 and 17 species in a single morning. Ralph et al. (1995) showed that, in comparable environments, sampling bird songs in-situ for 15 minutes should detect more than 90% of the bird species actually present.

Proposed causal model

Based on the information presented in the introduction, an initial causal model was created. In this initial model, horizontal productivity was hypothesized as the driver behind both horizontal heterogeneity and vertical productivity, whereas vertical heterogeneity was driven solely by vertical productivity. In other words, on both scales, heterogeneity is driven (or limited by) productivity, and the link between the two scales comes from horizontal productivity. As suggested by the literature review, all four environmental variables were hypothesized as possible drivers for bird species richness (Fig. 1).

Statistical analyses

As our data was regionally structured at the area level and the shape of the various relationships was of prime interest, the causal model could not be easily analysed with the usual path analysis methods (e.g. Shipley, 2000). Instead, as proposed by Shipley (2009), each independence claim suggested by the causal model was individually modelled, and the p-value of each claim was then used in the calculation of the overall d-separation test. Every independence claim was modelled with a general additive model (GAM) fitting a thin-plate spline with penalized regression splines using the mgcv package version 1.8-27 (Wood, 2011) package in R. To account for various confounding factors at the regional scale (size of the species pool, site history, etc.), a random intercept term for the area was also added to each model. This random intercept term also accounts for any differences in weather between the various recording days that could affect mean species richness in a particular area. Because of major asymmetries in their distributions, both horizontal and vertical heterogeneity variables were log-2 transformed before their inclusion in any models to stabilize variances. Finally, whenever the dependent variable in the models was bird species richness, it was modelled with a log-link and a Poisson error structure instead of the default identity-link with Gaussian error.

RESULTS

To understand bird species richness and its drivers, the initial model defined above (Fig. 1) was tested against observational data. Once accounting for the probable dependency structure between heterogeneity and productivity components (and possible confounding effects at the regional scale), the only driver to which birds seem to directly respond (the proximal cause) was horizontal heterogeneity (Fig. 2), whereas all other direct links to bird species richness needed to be eliminated. Specifically, in a model explaining bird species richness with all four hypothesized driving variables, the only term significantly related to species richness was horizontal heterogeneity (p-value = 0.029), whereas the remaining ones (i.e. vertical productivity, horizontal productivity and vertical heterogeneity) were not significantly related (p-values respectively 0.274, 0.837 and 0.367). Additionally, a dependency between vertical heterogeneity and horizontal productivity (independent of its vertical counterpart) was detected, which we did not hypothesize above, so it was subsequently added to the causal model. Once these modifications were made, confirmatory path analysis showed no evidence that this modified causal model could not have generated the data collected (d-separation test; C = 8.598, df = 10, p-value = 0.571).

The final conceptual model (Fig. 3) thus shows that the main driver behind productivity and heterogeneity variables is horizontal productivity, and because of its strong and constrained relationship with horizontal heterogeneity (Fig. 4), horizontal productivity can be considered as the ultimate driver of bird species richness.

DISCUSSION

The above results suggest that, in order to understand observed patterns of species richness, one must account for the possible relationships between the hypothesized drivers. The final conceptual model proposed herein (Fig. 3) suggests that, observed individually, any of the two drivers (heterogeneity, productivity) at any scale (vertical, horizontal) would have been related to species richness, although species richness directly responded only to horizontal heterogeneity. This finding is particularly illuminating, considering the confusing variety of patterns that have been observed with species richness in the past decade and our apparent incapacity at synthesizing them.

Knowing the above, one could conclude from a conservation perspective that once we’ve correctly parameterized the productivity-heterogeneity relationship, we could measure a single variable and infer the value of the other, going back to a bivariate model. This would simplify greatly the construction and interpretation of species richness models if, in fact, only one of the variables needed to be measured. On the other hand, it means that in any particular site where the landscape was artificially moved away from the typical productivity-heterogeneity relationship (e.g. by human development), assessment using only a single metric could be misleading.

At this point, we need to emphasize that, although we did not find independent effects of vertical heterogeneity and productivity (at any scale), we should not rule out that these effects indeed exist. Considering the natural variability of bird communities (Maron et al., 2005), our study included a relatively limited number of sites. Knowing the sheer number of studies that were previously able to highlight these relationships in the past (e.g. Seto et al., 2004; Koh et al., 2006; Huang et al., 2014), one should keep an open attitude about the existence of their independent effects on species richness and retest the above framework in as many contexts as possible.

As of yet, it is premature to affirm the generality of the highly constrained relationship between productivity and heterogeneity observed here. Many factors could affect its shape such as human interventions and historical contingencies. Nevertheless, we firmly believe that the careful study of the constraints between species richness drivers could deliver much deeper insights than simply synthesizing bivariate relationships as ecologists have done in the recent past.

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TABLES

Table 1. Information about the five forested areas studied in Quebec, Canada.

Area	Vegetation zone	Bioclimatic domain	Latitude	Longitude	n
Chibougamau	Continuous boreal forest	Spruce-moss	49°47' N	74°3' W	15
Abitibi	Continuous boreal forest	Balsam fir - white birch	48°8' N	79°25' W	18
Bic	Mixed forest	Balsam fir - yellow birch	48°20' N	68°47' W	18
Mauricie	Hardwood forest	Sugar maple - yellow-birch	46°46' N	72°50' W	17
Sutton	Hardwood forest	Sugar maple - basswood	45°4' N	72°30' W	19

FIGURES

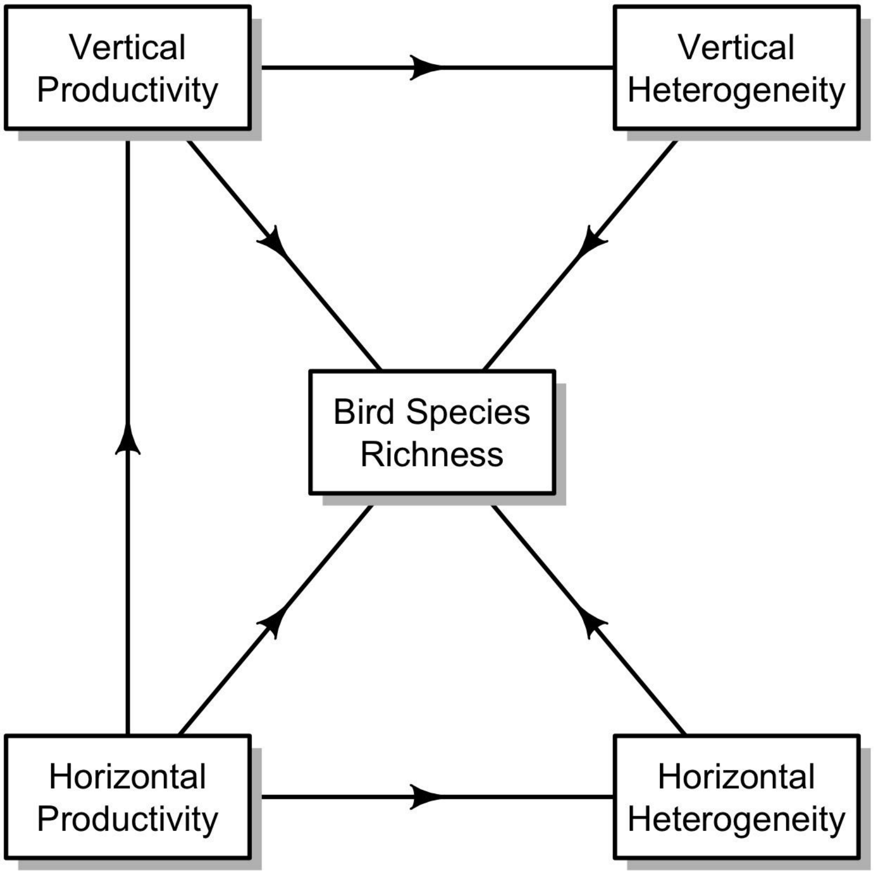

Fig. 1 Initial conceptual model, illustrating the hypothesised causal relationships between heterogeneity, productivity and bird species richness.

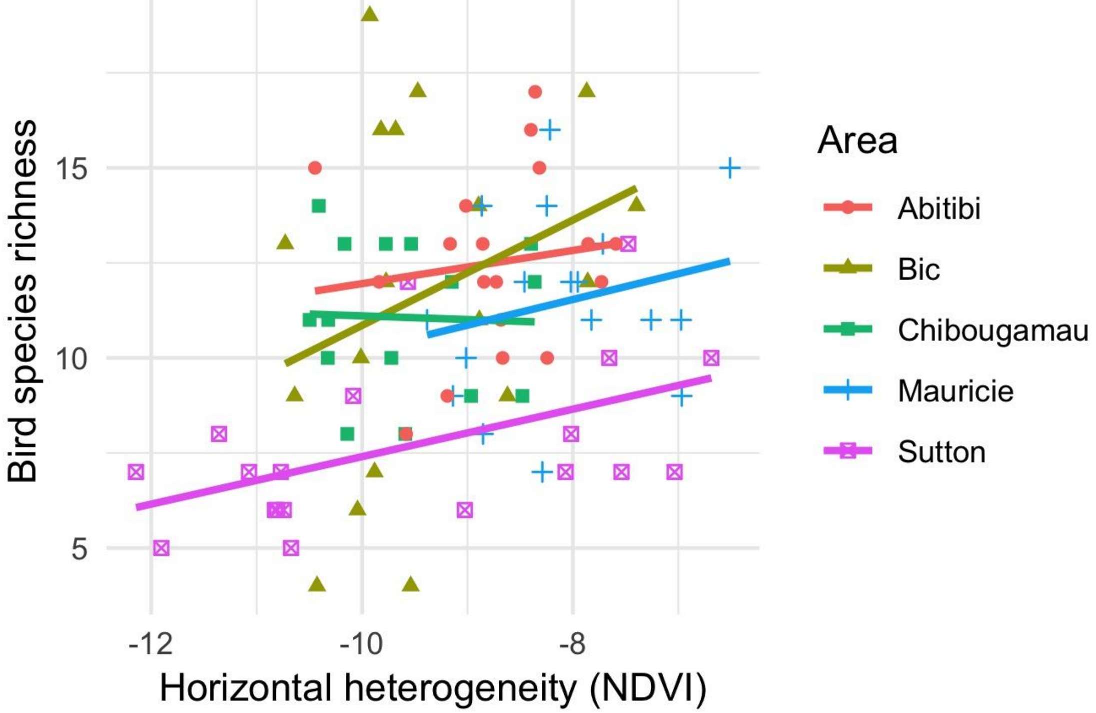

Fig. 2 Relationship between bird species richness and horizontal heterogeneity, as measured with NDVI variance, in 87 sites from five forested areas in Québec, Canada. Horizontal heterogeneity was log-2 transformed to stabilize its variance.

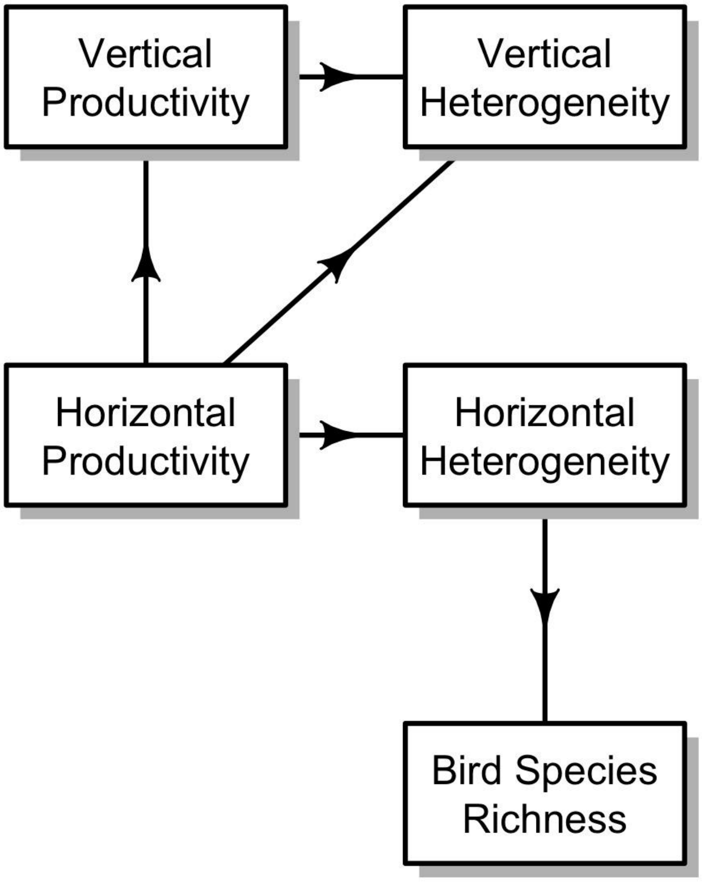

Fig. 3 Final conceptual model, illustrating the observed causal relationships between bird species richness, heterogeneity and productivity.

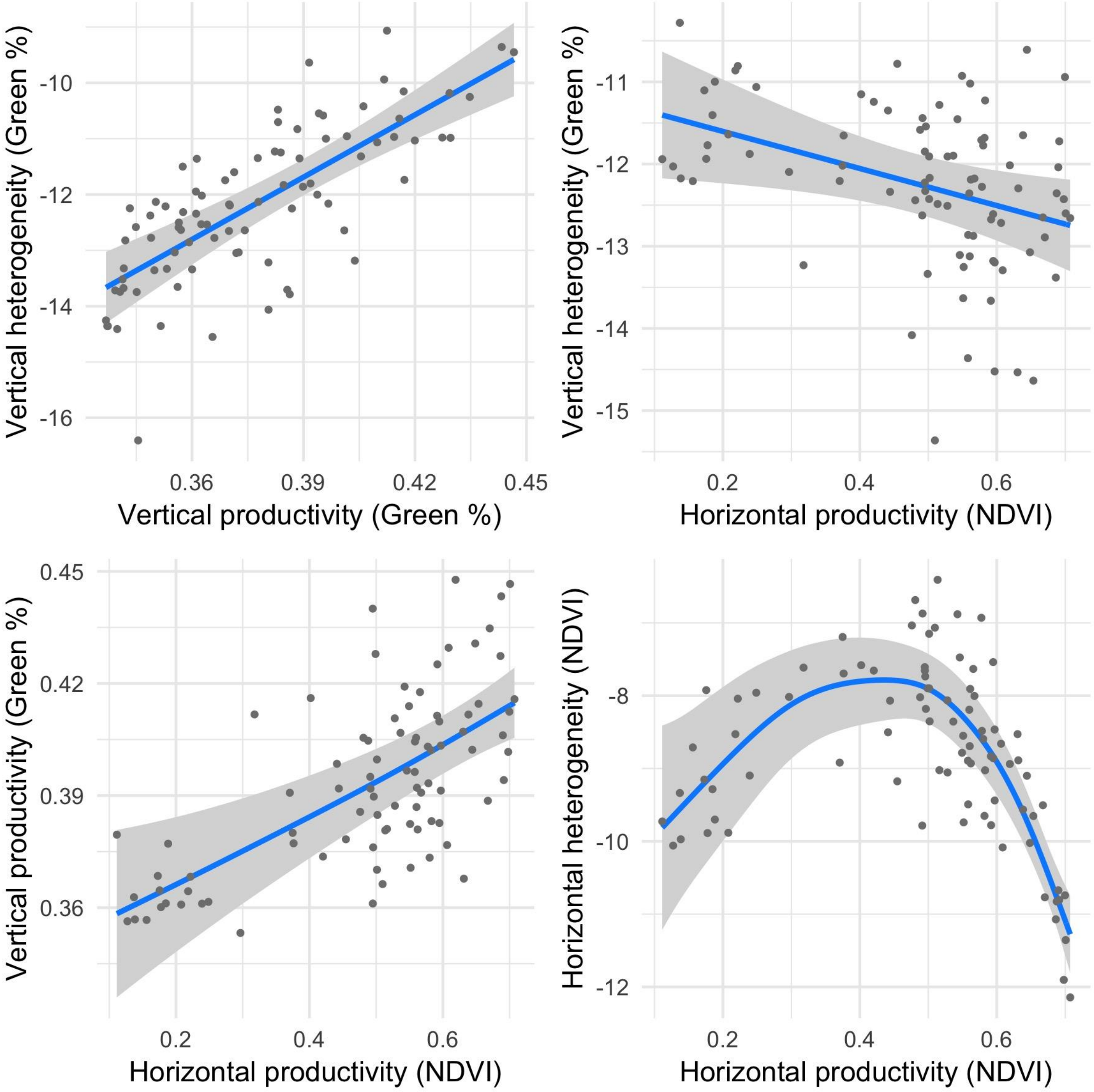

Fig. 4 Relationships between heterogeneity and productivity variables in 87 sites from five forested areas in Québec, Canada. Heterogeneity is measured as the variance in that respective scale productivity measurement (either NDVI or Green %). Heterogeneity measures were log-2 transformed to stabilize their variance. Each plot corresponds to an arrow in Fig. 3.

CHAPTER 6

LEVEL-2 ECOLOGICAL INTEGRITY: ASSESSING ECOSYSTEMS IN A CHANGING WORLD

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Abstract

Ecological integrity is a term often used to describe the state of ecosystems subjected to anthropogenic pressures. It is usually defined closely to the literal definition of integrity: being whole or unimpaired. Considering the deep changes our world is undergoing, we argue here for ecological indicators that are not restricted to naturalness targets. We propose a conceptual framework for so-called level-2 indicators of ecological integrity, that evaluate how the integrity of ecosystems is preserved given their naturalness context. We develop reference relationships between indicator and contextual variables and then assess how an ecosystem is doing, compared to others in similar contexts, by its distance to this reference. We explore two such relationships: the amount of aboveground phytomass an ecosystem stores in a given volume (biomass packing efficiency) and the mean patch size given the total habitat amount in the landscape (habitat connectivity). Using datasets at the national and worldwide scale, we show that these indicators are objective measures of ecological integrity that allow the comparison of plant stands and landscapes across different environmental and naturalness contexts. This framework provides a basis to evaluate if the state of an ecosystem is degrading and paves the way to a triage system prioritizing conservation and restoration actions.

Keywords : ecosystem health; ecological indicators; ecosystem triage; biomass packing; landscape fragmentation; connectivity

INTRODUCTION

Ecological integrity is a term often used to describe the state of an ecosystem subjected to anthropogenic pressures. It is usually defined quite closely to the literal definition of integrity: being whole or unimpaired. Similar definitions date back to the early ecological movement in the middle of the 20th century, where Aldo Leopold famously wrote: “A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise” (Leopold, 1949). These principles are now integrated in many acts and regulations around the world, with wordings like: “Ecological integrity means [...] a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes” (Canada National Parks Act S.C. 2000, c. 32). Ecological integrity is thus equated to naturalness, a concept on which hundreds of ecological indicators have been defined (Jørgensen et al., 2005; Kandziora et al., 2013; Niemi and McDonald, 2004). All indicators summarized in the above references more or less share the same goal: to evaluate how close an ecosystem is to the state it would be in the absence of anthropogenic pressures.

In this letter, we argue for the necessity, in a changing world, to develop measures of ecological integrity that are not only oriented toward naturalness. We propose a conceptual framework for so-called level-2 indicators of ecological integrity and suggest simple metrics that could achieve this goal.

THE NEED TO GO BEYOND NATURALNESS

There is little doubt that humanity has caused profound changes to the Earth's climate and land use since the middle of the 20th century (IPCC, 2013). However, we currently do not have the capacity to stop these changes, let alone revert back to pre-industrial states in the foreseeable future. In addition, global environmental changes and increasing human trade and travel around the world have often irreversible consequences on biological invasions (Dukes and Mooney, 1999; Levine and D'Antonio, 2003), which means that non-indigenous species are added to local flora and fauna at an alarming speed. Despite our best efforts, there is little to suggest that we can revert these changes with reasonable efforts (Vince, 2011); some authors going as far as calling this state of affairs "the new normal" (Marris, 2010), or "shifting baselines" (Pauly, 1995). Speciation and extinction events have always been a part of Earth's diversity history. Nevertheless, we are now facing a situation where, if most species currently declining become extinct, we would be experiencing a crisis similar to the five major extinctions, when approximately 50% of all living species disappeared (McKinney and Lockwood, 1999). Extinct species cannot be easily brought back to life without major ethical and financial costs (Jørgensen, 2013; Sherkow and Greely, 2013). None of the above factors (i.e., climate change, distribution shifts, mass extinctions) can be realistically reverted back to pre-industrial levels. Time is thus ripe to acknowledge that we are living in a changing world. We cannot expect an ecosystem to be whole or unimpaired anymore, if that definition means "as the ecosystem was in the past" (Wurtzebach and Schultz, 2016).

Many efforts have been made to save wildlife areas and large networks of protection areas have been implemented in the past 50 years. As of now, we are moving toward the goal to conserve whole or unimpaired ecosystems with an estimated 14.7% of the world's terrestrial and inland water ecosystems already under protection. We are thus 2.3% shy of the 2020 target deemed essential to the support of biodiversity (UNEP-WCMC and IUCN, 2016). Encouraging in a sense, these numbers also highlight the fact that, despite worldwide concerted efforts, there is a very low ceiling to the area that can be protected from human impacts. Furthermore, many sources have also been documenting biodiversity decline within the borders of protected areas (Brashares et al., 2001; Jones et al., 2004; Woodroffe and Ginsberg, 1998).

Moderately impacted ecosystems can still be major contributors to the maintenance of biodiversity and ecosystem functioning (Tscharntke et al., 2005; Van Buskirk and Willi, 2004). However, at this time, we have no means to determine which of these ecosystems are coping well and which require our immediate attention. Acknowledging that we cannot keep everything pristine, we need a way to determine how an ecosystem is performing, given its naturalness context, such as to prioritize our conservation actions. We describe below a second level of indicators, nested in the classical definition of integrity, which we will call level-2 measures of ecological integrity.

KEYS TO A USABLE DEFINITION OF LEVEL-2 ECOLOGICAL INTEGRITY

The first criteria that any measure of level-2 ecological integrity must fulfill is to account for the level-1 integrity of the ecosystem. It must be able to distinguish between an ecosystem that is subjected to anthropogenic pressures, but adapted to the “new normal”, and another one that is not coping well with these changes. The ranking must be clear: level-2 ecological integrity measures how an ecosystem is performing, given its naturalness context, never how bad its context is.

A second criteria that level-2 ecological integrity should meet is that of an objective measure. If we want to know how well an ecosystem is doing, we must refer only to the ecosystem itself and not over- or under-value the services we wish to extract from it. Ecosystem services are thus ruled out of level-2 integrity assessment, because different societies will expect different services from the same set of resources. A mature forest could rightfully be used as building material, or as a carbon sink, without any absolute way to prioritize between these uses. Note that these services, just as many level-1 ecological indicators, may have their rightful place in well-conceived management plans. We mainly wish to highlight that their prioritization level is not necessarily objective. Being objective also means that we cannot use past conditions as a reference to evaluate the state of an ecosystem, because in a changing world, it may be counterproductive to define what are the correct reference conditions. Is it the conditions from 50 years ago? 1000 years ago? Answers to these questions are open to ongoing debates that level-2 measures of ecological integrity must avoid.

A third and final criteria that level-2 ecological integrity should aim for is to be as context-agnostic as possible. As stated previously, level-2 ecological integrity must allow the comparison between ecosystems in different environmental and naturalness contexts. For example, many indicators of ecological integrity, like biodiversity or primary productivity, change from one ecosystem to the other, even if ecosystems are considered close to their state of naturalness. This last criteria invalidates most classical measures of ecological integrity (Baldocchi, 2008; e.g. Karr, 1981; Lindenmayer et al., 2000; Raffaelli and Mason, 1981), as they are, more often than not, defined for a specific local context, and are simply not applicable elsewhere.

CONCEPTUAL FRAMEWORK

One way to account for context when comparing different measures is through standardization. Comparing the condition of biological units after accounting for context-specific differences has a long tradition in ecology. With either Fulton's condition factor (Ricker, 1975), or one of its recent versions (i.e. Peig and Green, 2009), the underlying principle remains the same, which is to assess some indicator variable of interest irrespective of scaling effects. For instance, ecologists will study a large number of fish (or some other animals) from a population to establish the reference relationship between fish size and weight. Subsequently, the body condition of any individual from that population is assessed according to its deviation from the reference relationship. The animal will either be in better (above the relationship) or worse (below the relationship) condition than the average animal of a given length from that population. Although useful and still in use, length-weight relationships often differ quantitatively between taxa, regions, or development stages and thus do not meet the transferability criteria set above for level-2 ecological integrity measurements (see Martin et al., 2014).

The idea of standardizing indicator variables has also been applied to ecosystems. In a seminal paper, E. P. Odum (1969) proposed a series of development indicators based on energetic rates (e.g. production to respiration ratio [P/R], production per standing crop biomass [P/B]), which are predicted to increase through ecosystem maturation. This idea was already present in Margalef's work (1963), which stated that the relative amount of energy needed to maintain an ecosystem should be reduced as complexity of the energy throughflow increases. The P/R relationship replaces a reference state with a reference relationship to obtain a measure of ecosystem efficiency. Whereas productivity is highly variable among ecosystems, its ratio with respiration remains fairly steady throughout the productivity gradient (Baldocchi, 2008). However, from an operational standpoint, ecosystem productivity and respiration measures are not easily obtained. Where such measures exist, the P/R ratio is a good indicator of logging, draining or mowing disturbances (Baldocchi, 2008).

In this letter, we propose that level-2 ecological integrity could be conceptualized as the departure from a reference relationship between an indicator variable of interest and a contextual variable that describes the situation-dependent state of an ecosystem, including its level-1 ecological integrity. Departure from the reference should identify ecosystems that are more or less efficient structures than the average standard. Once such relationships have been described (see next section), level-2 ecological integrity can be measured in terms of deviations relative to this reference. Ecosystems further from the reference relationship are those that require our immediate attention in an analogy to a triage system. Additionally, it provides an objective measure to determine if the state of an ecosystem is degrading or improving over time.

EXAMPLES OF LEVEL-2 INTEGRITY INDICATORS

At the stand level

Plant biomass accumulation is a variable of primary interest that controls the fluxes of fundamental elements on Earth. For plant biomass to accumulate, a community needs sufficient light, water and nutrients, as well as an appropriate species pool to take advantage of the local conditions. Biomass changes are thus synthetic measures for all these biotic and abiotic constraints. Since aboveground plant biomass is structurally limited by plant height, and plant height is conditioned by disturbance regime, development stage and resource limitation (light, water, nutrients, etc.), the environmental context could be accounted for once biomass accumulation is standardized for stand height. In this framework, plant stand height becomes our contextual variable (how big are the plants here?) and aboveground biomass our indicator variable of interest (how much carbon the plant stand stores?). The standardization of mass by height for any plant community would provide a measure of biomass packing; that is, the amount of aboveground plant material that can be packed per unit volume.

We investigated the generality of the relationship between the height of vegetation stands and their aboveground dry biomass, to assess its potential as a level-2 ecological indicator. From a dataset of 971 plant stands gathered from 12 studies around the globe (see Proulx et al., 2015 for dataset details), we showed that both community biomass and height are dependent on their specific environmental context (Fig. 2). Nonetheless, when looking at the global relationship between these two commonly measured variables, one finds a consistent relationship (Fig. 3), suggesting that the amount of aboveground plant biomass is constrained by the stand height. An earlier assessment of biomass packing showed that ratios above 5 kg m^{-3} are probably not sustainable by natural communities, implying the existence of a limiting envelope to the relationship (Proulx et al., 2015, dashed blue line in Fig. 3).

A preliminary assessment of the biomass packing suggests that the height-biomass relationship of vegetation stands is also robust across both air temperature and soil fertility gradients (Proulx, submitted). This implies that, irrespective of the environmental or naturalness context, processes that enable coexistence may constrain the amount of aboveground plant biomass stored per unit volume (Proulx et al., 2015). Biomass packing (the standardization of aboveground biomass by stand height) could provide an easily measurable index of the efficiency of a plant community at storing carbon in aboveground tissues. A similarly general, strong and linear relationship between aboveground biomass and plant height was revealed on an independent dataset of 75 vegetation stands from different environmental contexts (Franco and Kelly, 1998).

Although promising, the biomass packing relationship also presents some limitations, which must be accounted for appropriately. For instance, competition for resources can affect aboveground biomass and densities only in crowded plant communities. Biomass and stand height measurements thus need to be conducted at peak biomass, and cannot be used for year-round assessments, especially in climates with strong seasonality. Moreover, trees in younger stands tend to invest in height and only later, once the stand has matured, in trunk diameter (Henry and Aarssen, 1999). The latter phenomenon probably explains the clump of less efficient forest communities which are entering the reference relationship from below in our example (Fig. 3). Biomass packing is therefore sensitive to the definition of plant height, and care must be taken to measure canopy height in relatively homogenous stands.

At the landscape scale

At a larger scale, the “state” of landscapes can also be described in terms of reference relationships. One simple indicator variable at this scale is habitat connectivity (e.g. patch size, edge density). Changes in habitat connectivity may occur naturally, through disturbances, biome transitions, landform changes, or because of human-driven modifications to the landscape. Ecology has a long tradition of studying the impacts of habitat connectivity on populations and communities, going back to debates on the optimal spatial organization of natural reserves (Diamond, 1976, the SLOSS debate; 1975; Simberloff and Abele, 1976, etc.), to processes underlying the maintenance of species in patchy habitats (Levins, 1969; Pulliam, 1988; Wilson, 1992).

Habitat connectivity is strongly related to the amount of (semi-)natural habitat in the landscape, as any removal (or addition) of habitat changes the configuration of the patches. Habitat amount in this sense is usually defined as the area of land cover that can fulfil some species' needs. In many cases, the amount of habitat is interpreted as (and often confounded with) the amount of natural cover remaining in the landscape, although fundamentally, one species' inhospitable matrix can be home to another one. Some authors have nevertheless questioned whether habitat connectivity has effects on biodiversity that are independent of habitat amount (Fahrig, 2013; Martin, 2018). To account for differences between landscapes in different environmental contexts, mean patch size (the variable of interest) must be standardized by the amount of habitat (the contextual variable).

Very few authors have tested how strongly the mean patch size of habitats is tied to habitat amount in existing landscapes (Didham et al. 2012; but see Proulx and Fahrig 2010). To assess the usability of this indicator as a level-2 ecological integrity measure, we built a dataset to assess the strength and generality of the mean patch size-habitat amount relationship. We randomly selected 10,000 square landscapes of 25 km2 anywhere in the continental USA from the 2001 National Land Cover Database (NLDC, Homer et al., 2015). Random landscape coordinates were selected from a uniform distribution bounded by the latitude and longitude range of the continental USA. Landscapes consisting entirely of water were discarded during the sampling process. In each landscape, we calculated the forested area (a one-sided view of habitat amount) and the average size of forest patches (a measure of habitat connectivity). Similar definitions of habitat amount are widespread in the landscape ecology literature. We then re-inspected every landscape in the 2011 NLCD to explore the dynamics of this relationship ten years later.

By studying thousands of landscapes across the continental US, irrespective of their specific environmental context, a clear pattern emerges (Fig. 4). Habitat amount during this 10-year period is decreasing in most landscapes, as indicated by the direction of arrows. Yet, a surprisingly constrained relationship remains between habitat amount and mean patch size. There seems to exist a narrow amount of connectivity (i.e. mean patch size) that landscapes reach for a given amount of habitat, despite the variety of forces that act upon landscape development (e.g. Antrop, 1998). The constraints are particularly strong when considering the range of configuration patterns that man or nature could possibly achieve for a given amount of habitat (Fig. 4, dashed blue line forming the bottom of the envelope).

With our general reference relationship in hand, we can now look at it as a level-2 integrity indicator (mean patch size standardized by habitat amount). Although it is clear that protecting more habitat is a reasonable conservation target (level-1 ecological integrity), different landscapes in contrasted environmental or naturalness contexts can be compared when looking at the deviation of mean patch size from the reference relationship. Considering that the relationship generalizes across different contexts, one can independently assess if patches are too small for the amount of habitat that remains in the landscape. Using different measures of habitat amount and connectivity, Proulx and Fahrig (2010) found a strong and general relationship between the two measures for landscapes all across Canada. Deviations from this relationship indicated that the process of agricultural development leads to a reduction in pattern variation (Proulx and Fahrig, 2010).

DISCUSSION

Level-2 metrics of ecological integrity could be applied to prioritize conservation and restoration efforts in novel, more nuanced ways. For example, the city council of a suburban town votes on a budget to improve the ecological integrity of one of its parks, and has to decide which one to restore. One park is in a downtown area. It is mostly concrete structures with few small patches of trees. The other park is in a forested area near the edge of the town and has more, and larger, patches of trees. For analysis purposes, we will consider these parks as small landscapes of equal size. Based on connectivity measurements (level-1 assessment), the downtown park would be the obvious restoration target, being the less natural one with smaller, less connected tree patches. On the other hand, level-2 metrics (i.e. standardized mean patch area per natural habitat amount) might point out that the forested park is the most in need of restoration, because compared to other parks with similar amounts of tree cover, the patches in this one are smaller. In this context, the level-1 and level-2 metrics would provide two different pieces of information. Level-1 informs us about how natural an ecosystem is, whereas level-2 helps us assess how modified an ecosystem is compared to others in similar contexts. Without level-2 assessment, the forested park might not see any restoration work before its tree cover is as sparse as the downtown one.

One drawback of using contemporary data points to construct reference relationships is that the current situation is considered as normal. It also means that the relationship between level-1 and level-2 indicators of integrity is dynamic, and may continue to shift through time. If humanity keeps altering ecosystems more and more, the target for a typically connected landscape will only get lower and lower. This moving target should be taken as a reminder that we ultimately control the fate of ecosystems on Earth. It is, again, all about priority management.

Through refining the set of reference relationships to the point where they are useful to compare ecosystems and set management priorities, conservationists will also be facing novel moral dilemmas. By using an objective level-2 measure of ecosystem state, we put aside considerations about the presence of particular habitat structures, species, or communities of special interest. For example, if a popular recreational hunting species is declining and our integrity assessment indicates there is nothing particular to worry about, what should we do? Should we actively manage the ecosystem to preserve the species? Recognizing such circumstances will force us to be upfront about our motivations for protecting species or ecosystems of interest. We may need to acknowledge that sometimes we protect nature simply because we appreciate and value it (Vellend 2017).

CONCLUSION

Once Noah's Ark is full and we have saved some of nature's wonder, future management priorities will need to focus on ecosystems under moderate stress and disturbance. The more transformed and managed ecosystems are, the less useful level-1 assessment measures will become. The clock is ticking for scientists to develop level-2 measures of ecosystem integrity that are applicable in different ecosystems and environmental contexts. We believe that conservation research should focus on describing and testing widely applicable standardizing relationships in order to objectively set targets for level-2 ecosystem integrity. Rehashing the current pristine-or-anthropized indicators over and over could, before long, cause ecologists to lose the few sympathetic ears we have today.

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FIGURES

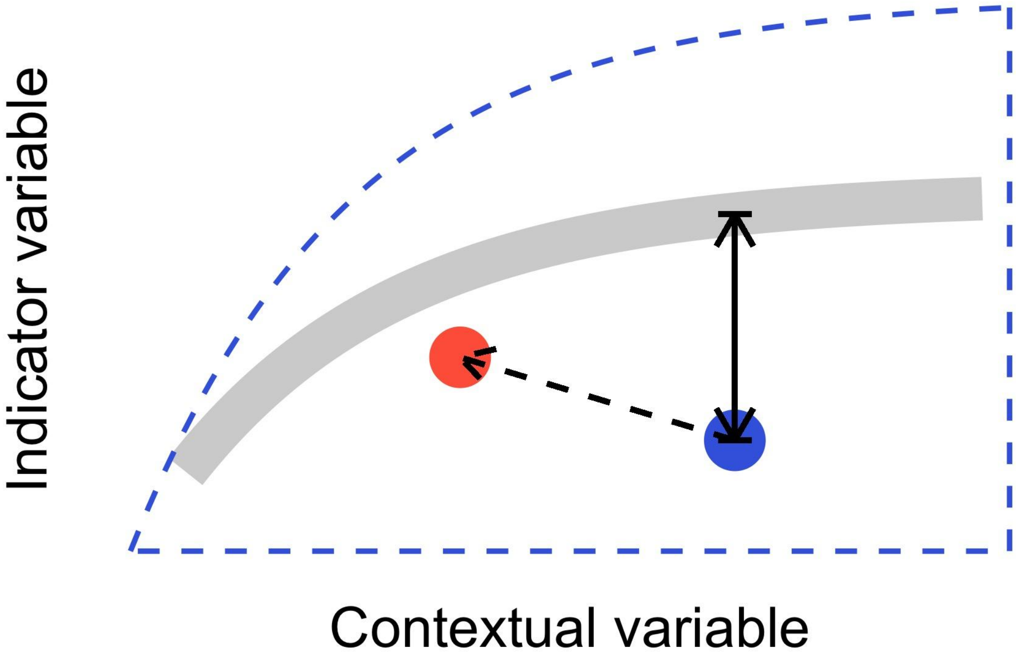

Fig. 1 Conceptual model of level-2 ecological integrity assessment from the standardization of an indicator variable with a contextual variable. Dashed blue line is the envelope enclosing all possible ecosystem states. Thick gray line is the reference relationship. Blue point is a particular ecosystem, with a particular deviation (its level-2 integrity deficit) from the reference relationship. Red point and corresponding dashed arrow is a possible trajectory the ecosystem could take, where despite a change of context, its level-2 integrity (deviation from the reference relationship) would improve.

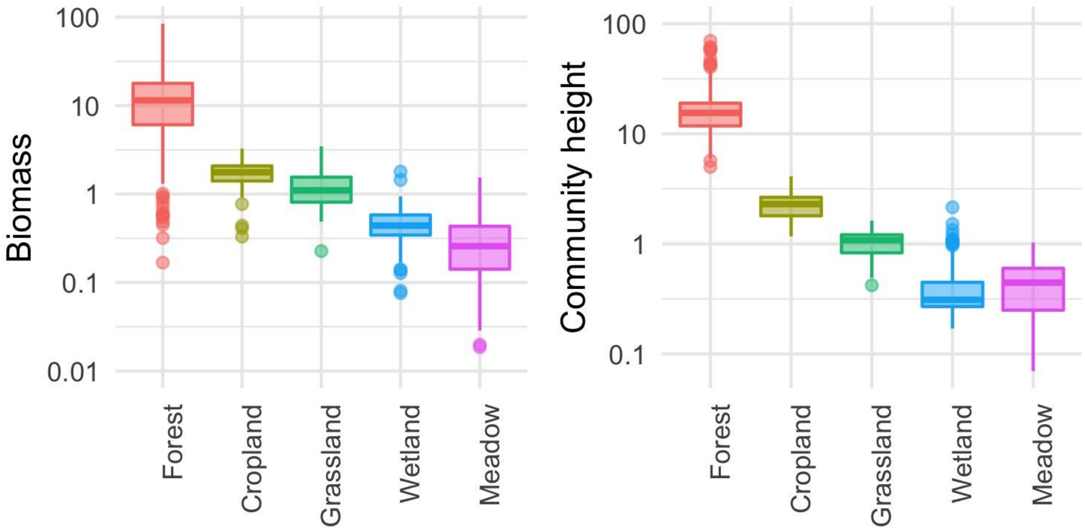

Fig. 2 Relationship between ecosystem type and (a) biomass (kg m^{-2}) and (b) community height (m) in 971 plant communities gathered from 12 studies around the globe. Boxes contain 50% of the data, with center line at median. Whiskers extend up to 1.5 interquartile range.

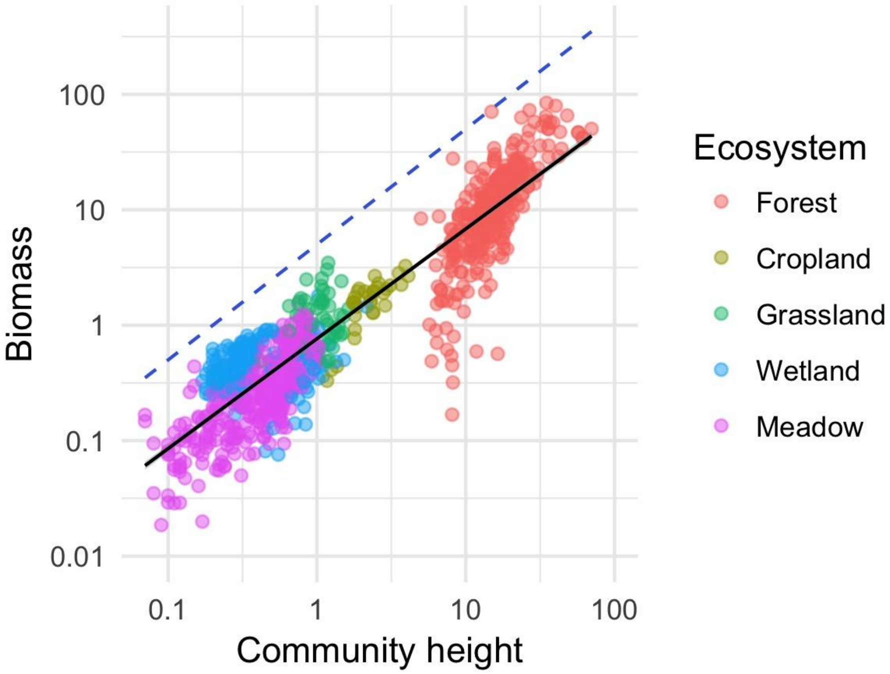

Fig. 3 Relationship between community stand height and aboveground biomass in 971 plant communities gathered from 12 studies around the globe in 5 ecosystem types. Biomass is measured in dry kg m^{-2}, community height is in m. Dashed blue line is the maximum achievable aboveground biomass for a given stand height in natural communities.

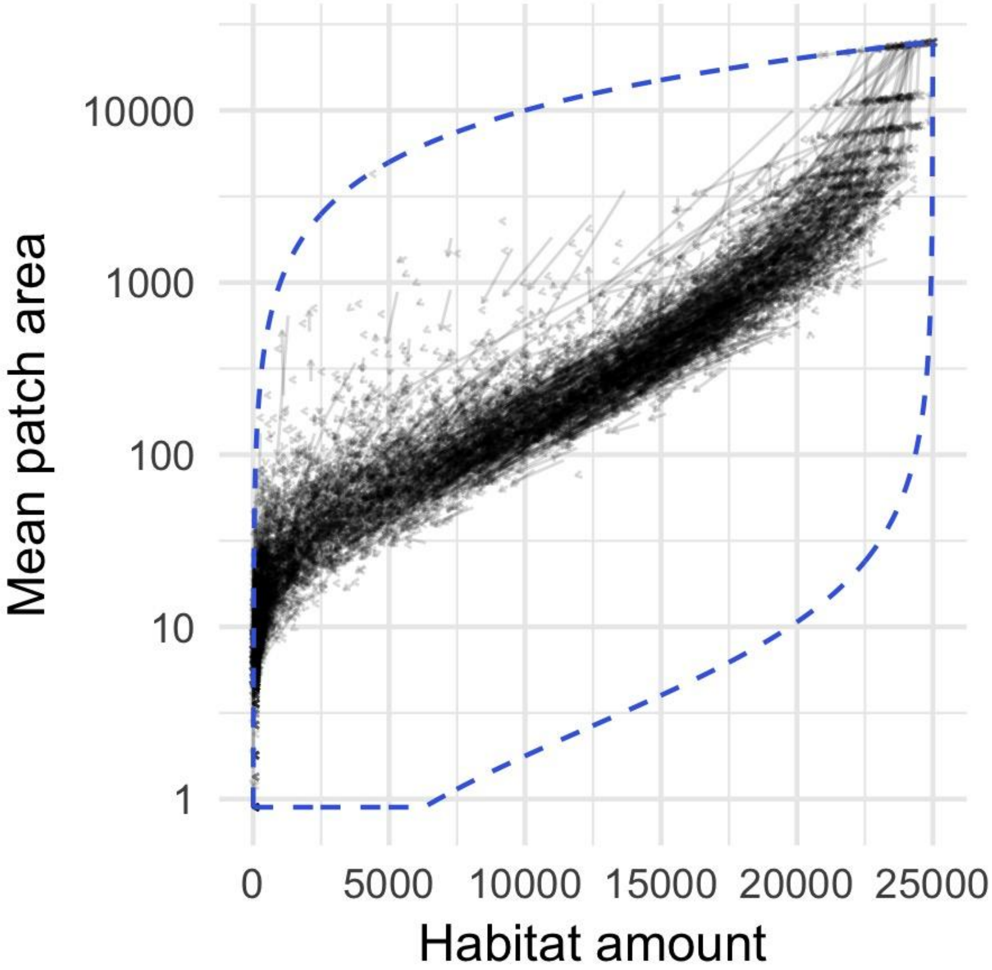

Fig. 4. Relationship between habitat amount (forested area; ha) and mean patch size (ha) in 10,000 randomly selected 25 km^2 landscapes across the continental USA. Arrows point from the 2001 configuration to the 2011 configuration of each landscape. Dashed blue line is the envelope defining all the possible configurations a landscape could take, limited at the top by a single patch using all the forested area, and at the bottom a checkerboard-like pattern forming as many habitat patches as possible for a given forested area.

CONCLUSION

SYNTHESIS AND SCIENTIFIC CONTRIBUTIONS OF THE THESIS

The above six chapters highlighted the many types of advances that can be achieved by striving for more generalities in conservation biology.

First and foremost, the application of pro-generalization techniques helped highlight nuances in our understanding of many biodiversity drivers. In chapter 1, we showed that bird diversity is an ever changing metric, that, in addition to previously known drivers such as productivity and heterogeneity, also changes across seasons and that the amplitude of this seasonal change itself is driven by its own set of variables. In chapter 3, we showed through a meta-analysis of multiple tests of the habitat amount hypothesis that, although the original idea was framed more or less as a yes-no binary question, the reality is that there is a clear, but somewhat weak effect of habitat configuration on species richness when controlling for habitat amount.

Another benefit of a quest for generalities, as suggested herein, is that more often than not, we come up with studies that are more robust and have more power. It is often difficult, both logistically and financially, to study large gradients or large amounts of sites in a single study. But if you make a conscious effort to look for generalities, you either make sure you have enough budget to study many ecosystems in a single study (as in chapter 5), or you combine together many existing studies or datasets (as in chapters 2, 3, and 6), or you harness the power of citizen science (chapter 1) to reach that goal.

Finally, looking for generalities means that often, we end up putting side by side things that were usually studied in isolation. This is what happens in chapter 2, where we tie in a single model the species richness of a community and the abundance of it’s most common species, only to highlight the fact that there exists a conservation compromise, where both values cannot be maximized at once. Sometimes, by combining attributes in a single model that are often studied separately, we can also highlight the potential confounding effects of the two attributes on a third one. This is what happens in both chapters 4 and 5, where we highlight the strong relationship between mean productivity and productivity variance, and show that their effects on species richness can easily be confounded if studied in isolation. Finally, in chapter 6, we highlighted that by trying to generalize the definition of ecological integrity across ecosystems and biomes, we are faced with a lack of usable metrics to properly compare ecological integrity in these situations, and that the only solution is to acknowledge that we need to revise our expectations and definitions. In these four cases, striving for generalities, although through highly different means, got us to the same general conclusion : there were no clear-cut answers to our original question. That the truth was more in the nuances of our interpretation than in raw numbers or answers.

The major contribution of this thesis is thus to showcase the variety of benefits that can be obtained by striving for more generalities in conservation biology, which are namely the added nuances in our understanding of biodiversity drivers, the discovery or clarification of compromises and confounding effects, as well as the side benefits of having more powerful and more robust studies.

RESEARCH PERSPECTIVES

GENERALIZING ACROSS SPECIES AND BIOMES

One way to increase the transferability (i.e. reduce contingency issues) of ecological studies and increase our understanding of biodiversity we have not discussed so far in this thesis is by replacing species identity in analyses with their respective functional traits and attributes (McGill et al., 2006). With such an approach, one would replace typical results like “Blue jays are more present in open spaces” to “larger, omnivorous birds are more present in open spaces”. Doing so unravels the selection and evolution forces at work in a system, instead of studying only the end-point of the processes (i.e. the current species abundances). Once again, with that approach as with many others aiming at reducing contingencies, one needs to study a broad enough environmental gradient and a wide enough variety of species for these types of conclusions to have any meaningful sense.

Traits-based ecology has made great breakthroughs in the past twenty years or so, in our understanding of the mechanisms behind many observed ecological patterns (Webb et al., 2010). This approach offers great potential, although it comes with an additional burden for the researchers. In particular, it is often highly time consuming to measure all the necessary attributes on each studied individual (in plant communities) or sometimes just outright impossible (e.g. in large-scale bird censuses like the North American Breeding Birds Survey). The common solution to this issue is often to replace individual measurements with the mean value measured on a sample of individuals from each species or a standard value found in the literature. Such an approach has potential drawbacks, especially because it erases out variability between individuals, which in some organisms can be very important (e.g. Carlucci et al., 2015; Stevens et al., 2010).

One recent advance to circumvent these scalability issues is to use some form of rapid assessment methods, such as extracting vegetation properties from photographic images, instead of measuring vegetation directly. As showcased in chapter 5, this method can be highly efficient, but, as of now, it is also less direct. It is often difficult to associate a particular photography metric directly with a measurable, physical property of the vegetation.

For example, in chapter 4, we ran into that issue when we wanted to work at large scales with remote sensing data. Although our initial conceptual model was centered around the heterogeneity-productivity question, we had to settle down on the more landscape-oriented measurements of natural vegetation cover and land-cover variance, because we did not have access to a reliable productivity metric from remote sensing products. The same issue also arises in chapter 5. Although intuitively we grasp that more productive plots or stands should appear greener in *in-situ* photographs or satellite images, there exists at this point no universal way to convert from one metric to the other in multi-species stands or across different land cover types. There is, thus far, a need to calibrate NPP calculations with ground-truth data for each vegetation type encountered (Scurlock & Prince, 1993)

For functional traits in animal species, we are even farther from automated traits description. Although it is possible to have size measurements on zooplankton individuals in water samples (Gorsky et al., 2010), we are very far from such successes with terrestrial vertebrates. In fact, we are barely scratching the surface on automatically detecting and identifying them in pictures (Weinstein, 2018), so we are still many steps aways from measuring functional traits on them.

For decades, machine learning has been doing an excellent job at classification tasks, where the data representation was fairly simple (i.e. rectangular datasets). On the other hand, highly perceptual tasks (language processing, image categorization, autonomous cars etc.) were still very hard problems for computers to solve merely a decade ago. With the development of deep learning algorithms (i.e. multi-layered neural networks with error back-propagation), the numerical representations of these problems have made huge steps forward. For example, the ImageNet Challenge, which consists of 1.4 million images to classify in the correct 1000 categories (Deng et al., 2009), was considered a very tough problem in 2011 with accuracy rates around 75 % for the best algorithms. Within four years, the arrival of deep learning meant the *difficult* task was now more or less solved, with accuracy rates reaching over 95 %. Experts on the subject predict that the actual revolution these new algorithms will bring to our lives has not yet happened, because we are barely beginning to understand how to apply these techniques to real-life problems. Those same experts also add the caveat that the field of artificial intelligence has been through this *hype* stage a couple of times before in its history, only to fall flat when reality caught it back (Chollet & Allaire, 2018). Nevertheless, I feel like ecology (and life sciences in general) has the potential to be a much different field of study ten or twenty years from now, when these technologies will be more commonplace, especially in tasks that are, as of today, deemed impossible to automate.

EVOLVING GENERALISATIONS

Although data synthesis in the form of a meta-analyses is a great way to recap all available data and increase to power devoted to specific ecological questions, they also present a major flaw as they are only snapshots, valid at the time of publication. For most of the history of science, this was mainly a non-issue. As of today though, where millions of scientific studies are published every year (Bornmann & Mutz, 2015), keeping scientific conclusions up to date is a real challenge, and meta-analyses are far from immune to that issue. As an example, the search query used for chapter 3, which returned 15 results at the time of writing the original manuscript, now returns 38 entries. Less than three years after publication, the number of potential studies for the meta-analysis has more than doubled.

With today's automated reporting tools that can be easily chained to the actual statistical analysis process (i.e. RMarkdown), producing near-real time syntheses should be fairly trivial. Notwithstanding the lack of standardized outlets for these kinds of real-time results, we are also faced with a resource problem : who should put the manpower into the constant process of validating new studies and entering them in the analysis system?

In conservation biology, a couple of organizations have been created to generate and aggregate syntheses, both in the fields of conservation (Conservation Evidence; www.conservationevidence.com) and environmental policies (Collaboration for Environmental Evidence; www.environmentalevidence.org). But, as far as we are aware, none of these organizations have taken it into their own hands to keep the syntheses current.

In health sciences, the Cochrane organization was developed for this exact purpose : not only to publish systematic reviews, but also to keep them current as new research is published. Although on its inception Cochrane had a clear goal of keeping all reviews current, the task has rapidly grown to an impossible size, which forced the organization to review their objective and revise every two years at first, and then finally, only on a priority basis (Garner et al., 2016).

So while I think conservation biology would greatly benefit from the creation of an organization dedicated to keeping syntheses up to date, I think there are great lessons to be learned upstream before that. In particular, before launching into such a project, there is a need to build a priority list of the most important questions in conservation biology. Newer questions will need to be updated more frequently, as the sample size for evidence is quite small and thus could easily be biased. Contentious issues will also need more frequent updates, as few new data points are needed to push conclusions on one side or the other while sitting on the edge. Already, there have been steps in that direction, with some authors establishing a list of the most relevant ecological questions for which we don’t have clear answers yet at the global (Sutherland et al., 2009) and national level (Rudd et al., 2011). How to prioritize through these lists is still up for debate, but should probably be the next logical step on a path to having more up to date syntheses in conservation biology.

CONCLUSION

The idea of producing generalizations in ecology is a much richer one than the simplistic process of trying to see if things always happen in the same way everywhere. As illustrated above, there are important insights to be gained from, not necessarily achieving general results, but by consistently striving for them.

As seen especially in chapter 6, there are very important ecological and philosophical questions that arise by putting things side by side. By comparing them and looking for common ways to assess them. Beside ecological integrity, there are many such topics in ecology today that would greatly benefit from these kinds of discussions.

In the study of invasive species and ecosystem restoration, there is a common thread where practitioners often wish to put things back as they were before the anthropocene. As explained in chapter 6, as we move further into the process of anthropizing Earth, both the existence of a pristine reference and the attainability of such a target will get more and more difficult. There is a very deep reflection that needs to happen about what we will do once it is clearly impossible to restore things to their pristine state. What are the common characteristics we feel nature should have in a human-dominated world? What generalizations can we extract from the places where we feel we do live mostly in harmony with nature as modern humans? This won’t be an easy discussion, and many *a priori* ideas will need to be left behind before we get there. But the sooner we’ll have these discussions, the better we will be prepared to tackle the future we have been building for 150 000 years.

Maybe conservation biology won’t find general rules as was once hoped, but clearly, looking for them would make conservation biology progress in a more nuanced and thoughtful way.

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