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Published online: 17 Mar 2022.

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Food biodiversity: Quantifying the unquantifiable in human diets

Giles T. Hanley-Cook[a]* (iD), Aisling J. Daly[b]* (iD), Roseline Remans[c] (iD), Andrew D. Jones[d] (iD), Kris A. Murray[e,f] (iD), Inge Huybrechts[g] (iD), Bernard De Baets[b] (iD) and Carl Lachat[a] (iD)

[a]Department of Food Technology, Safety and Health, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium; [b]Department of Data Analysis and Mathematical Modelling, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium; [c]The Alliance of Bioversity International and International Centre for Tropical Agriculture, Geneva, Switzerland; [d]Department of Nutritional Sciences, School of Public Health, University of Michigan, Ann Arbor, Michigan, USA; [e]MRC Centre for Global Infectious Disease Analysis, School of Public Health, Imperial College London, London, UK; [f]School of Hygiene & Tropical Medicine, MRC Unit The Gambia at London, Banjul, The Gambia; [g]Nutrition and Metabolism Branch, International Agency for Research on Cancer, Lyon, France

ABSTRACT

Dietary diversity is an established public health principle, and its measurement is essential for studies of diet quality and food security. However, conventional *between* food group scores fail to capture the nutritional variability and ecosystem services delivered by dietary richness and dissimilarity *within* food groups, or the relative distribution (i.e., evenness or moderation) of e.g., species or varieties across whole diets. Summarizing food biodiversity in an all-encompassing index is problematic. Therefore, various diversity indices have been proposed in ecology, yet these require methodological adaption for integration in dietary assessments. In this narrative review, we summarize the key conceptual issues underlying the measurement of food biodiversity at an edible *species* level, assess the *ecological* diversity indices previously applied to food consumption and food supply data, discuss their relative suitability, and potential amendments for use in (quantitative) dietary intake studies. Ecological diversity indices are often used without justification through the lens of nutrition. To illustrate: (i) dietary species *richness* fails to account for the distribution of foods across the diet or their functional traits; (ii) *evenness* indices, such as the Gini-Simpson index, require widely accepted relative abundance units (e.g., kcal, g, cups) and evidence-based moderation weighting factors; and (iii) functional *dissimilarity* indices are constructed based on an arbitrary selection of distance measures, cutoff criteria, and number of phylogenetic, nutritional, and morphological traits. Disregard for these limitations can lead to counterintuitive results and ambiguous or incorrect conclusions about the *food biodiversity* within diets or food systems. To ensure comparability and robustness of future research, we advocate food biodiversity indices that: (i) satisfy key axioms; (ii) can be extended to account for disparity between edible species; and (iii) are used in combination, rather than in isolation.

Introduction

If humanity is concerned about global food security and nutrition, then it should also be concerned about protecting and restoring the biosphere we inhabit (Food and Agriculture Organization of the United Nations 2019). "Eat a variety of foods" or dietary diversity is a longstanding public health recommendation to achieve a nutritionally adequate diet (Herforth et al. 2019). More recently, sustainable healthy diets have been defined as "dietary patterns that promote all dimensions of individuals' health and wellbeing; have low environmental pressure and impact; are accessible, affordable, safe and equitable; and are culturally acceptable" (Food and Agriculture Organization of the United Nations and World Health Organization 2020). Biodiversity loss of both wild and agricultural species can have detrimental

effects for both diet quality and the environment, by reducing the availability of and access to a diversity of nutritious, seasonal foods, and by contributing to the loss of ecosystem functions (e.g., nitrogen fixation by legume-rhizobia symbiosis) (Myers et al. 2013; Heilpern et al. 2021).

Biodiversity is broadly defined as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity *within* species, *between* species and of ecosystems" (United Nations 1992). At present, approximately 21% of plant (Food and Agriculture Organization of the United Nations 2010) and 17% of animal species are at risk of extinction (Food and Agriculture Organization of the United Nations 2015). Distinct edible species and varieties, *between* and *within* food groups, offer a large spectrum of nutritional

benefits (Barabási, Menichetti, and Loscalzo 2020), as these foods contain diverse compositions, quantities, and densities of essential macro- and micronutrients (e.g., protein, iron), bioactive non-nutrients (e.g., phytochemicals), and anti-nutrients (e.g., tannins) (Burlingame, Charrondiere, et al. 2009; Burlingame, Mouillé, et al. 2009). Nutrient content differences *within* crop varieties (Kennedy and Burlingame 2003) and animal breeds (Medhammar et al. 2012; Barnes et al. 2012) of the same species can be even greater than the differences *between* species (Lutaladio, Burlingame, and Crews 2010). Yet, from the approximately 7,000 crops and several thousand animals used by humans for food, only 12 crops together with 5 animal species currently provide ~75% of the world's food energy supply (Food and Agriculture Organization of the United Nations 2010). In Europe, beef, wheat, pork and potato alone account for ~45% of self-reported dietary kcal intake (Hanley-Cook, Huybrechts, et al. 2021).

Biodiversity loss is the boundary where current rates of extinction (100 to 1,000 times the natural "background" rate) put planet Earth furthest outside the "safe operating space for humanity" (Rockström et al. 2009; Steffen et al. 2015). Land conversion, in particular for industrial mono-crop and animal agriculture, is a major driver of habitat loss, degradation, and encroachment, which, along with direct killing (e.g., overharvesting), continue to be leading threats to biodiversity (Maxwell et al. 2016). Food species biodiversity delivers a multitude of ecosystem services (e.g., human health and culture) (DeClerck et al. 2011), reduces pressures on single species (e.g., the Panama disease threatens the Cavendish banana, which alone is responsible for 40% of global banana production) (Dale et al. 2017), and helps to maintain food and nutrition security in the face of (anthropogenic) stressors and recovery from and adaptation to these disturbances (Díaz et al. 2019).

Notwithstanding the best intentions of global and local implementation of food diversification and conservation strategies (e.g., land sparing and sharing, Svalbard Global Seed Vault, Swedish food-based dietary guidelines, Chefs' Manifesto, Slow Food's Ark of Taste) (Hanley-Cook, Kennedy, and Lachat 2019) escalating human stressors continue to drive extinctions, wild species population declines, and habitat destruction continues at large scales (Maxwell et al. 2016; Tittensor et al. 2014; Dirzo et al. 2014; Pimm et al. 2014). Moreover, over the past decades, agricultural policies have often focused on improving the yield of key staple cereal crops; mainly rice, wheat, and maize (Pingali 2015). Subsequently, the composition of global food supplies and diets have become more homogeneous, comprising an ever smaller number of edible species (i.e., variation between countries' food supplies has declined by ~70% over the last 50 years) (Khoury et al. 2014).

The increased recognition of inter-relationships between human and planetary health effects of food has resulted in a proliferation of interest in integrated conceptual frameworks (High Level Panel of Experts on Food Security and Nutrition 2020; World Health Organization 2020) and joint analyses of environmental and nutrition outcomes (Johnston, Fanzo, and Cogill 2014; Clark et al. 2019; Springmann et al. 2018). However, although hunger, food security, and sustainability are addressed in the Sustainable Development Goals (SDG), the current indicators used for SDG 2, 12, and 15 consider nutritional status (e.g., under-five stunting or anemia in women, rather than upstream food intake), sustainable management of terrestrial ecosystems, and agricultural sustainability separately (United Nations 2020). Furthermore, while food biodiversity is inextricably linked to human nutrition (Golden et al. 2011; Penafiel et al. 2011), it is not systematically assessed from dietary intake (Food and Agriculture Organization of the United Nations and Bioversity International 2017) or national food production or supply data collection efforts (Remans et al. 2014). At present, questionnaires including validated food group diversity scores for women (Hanley-Cook, Tung, et al. 2020) and children (Choudhury, Headey, and Masters 2019) are being enumerated around the globe (e.g., Demographic and Health Surveys, Gallup World Poll) to feasibly monitor and evaluate dietary patterns, yet their linkages with biodiversity are not explicit.

Cross-cutting studies attempting to assess the reciprocal links between landscape biodiversity, food production diversity, and dietary intake have used various diversity indices without validation through the lens of nutrition or ecology (Jones 2017; Berti 2015). The level of taxonomic detail collected during dietary intake assessments is potentially a key bottle-neck (i.e., often lacking data on species, varieties, or cultivars) for evaluations of biodiversity cascades across scales (e.g., from landscapes to microbiomes) (Remans et al. 2015). To clarify, consider conventional dietary diversity scores (Supplementary material, Table S1) and food variety scores; the latter do not separate mixed dishes into all their ingredients, but do distinguish between e.g., low *vs* high fat products (Drewnowski et al. 1997), which are used as proxies for diet quality and measure the diversity of (a limited number of) food groups or food items consumed (Miller et al. 2020). Neither of these groups of diet indices specifically captures the (complementary) nutritional variability and ecosystem services (e.g., finite genetic resources) provided by dietary *species* richness and dissimilarity *within* food groups (explicitly recommended in e.g., Dietary Guidelines for Americans 2015-2020), and moderation *between* or *within* food groups (Hanley-Cook, Kennedy, and Lachat 2019). To conceptualize this link, the notion of *food biodiversity* was coined by researchers and defined as "the diversity of plants, animals, and other organisms (e.g., fungi, insects) used for food, both cultivated and from the wild" (Food and Agriculture Organization of the United Nations and Bioversity International 2017; Lachat et al. 2018).

Any (semi-)quantitative study of food biodiversity, no matter which aspect or scale is of interest (e.g., food system, farm, diet), will involve its measurement. In dietary assessment, this is a complex task both conceptually and practically: food classification is dependent on the level of *a priori* defined detail in food frequency questionnaires (Hanley-Cook, Huybrechts, et al. 2021) or respondents' ability to recall short-term consumption (Lachat et al. 2018), while food

composition data is limited for many underutilized, neglected, and even common species (Charrondière et al. 2013). Hence, biodiversity is usually quantified by constructing mathematical functions known as *ecological diversity indices*. The computation of such indices from dietary intake (or food supply) data permits comparisons between e.g., population groups, geographic regions, seasons, functional food groups, or taxa (species) (Food and Agriculture Organization of the United Nations 2021).

However, in ecology, there is a lack of user guidance on which (combination) of the numerous biodiversity indices are more suitable and informative than others (Daly, Baetens, and De Baets 2018). This challenge is just as acute in nutrition, where construction of e.g., simple, population-group specific food group diversity scores often diverge in number and aggregation of subcomponents and minimum intake cutoffs (Martin-Prevel et al. 2017; Hatløy, Torheim, and Oshaug 1998; Vandevijvere et al. 2010; Kant et al. 1993; Ponce, Ramirez, and Delisle 2006). The available diversity indices are so numerous and varied in their nutritional (and ecological) interpretation and mathematical behavior that we must start by asking ourselves the most fundamental question: what is actually meant by *food biodiversity*? This narrative review aims to provide guidance to researchers seeking to use established *ecological* diversity indices in (quantitative) food intake studies. Therefore, our study focuses on the fundamental characteristics of (food) biodiversity indices, which have consequences for their use and, perhaps more importantly, their misuse in nutritional epidemiology.

Conceptualizing food biodiversity

The mechanisms driving relationships between food biodiversity and human or planetary health are considered to be mainly due to three processes (Hanley-Cook, Huybrechts, et al. 2021; DeClerck et al. 2011). The first is known as the *sampling effect* and assumes that as diversity increases there is a greater probability, simply by chance, of including a highly nutritious or productive species. The second mechanism is the *complementary effect*, in which (chemical or physical) interactions between food species (e.g., black bean and maize) result in a function or yield greater than expected by chance (i.e., over-yielding) (Liu 2003, 2004). The third mechanism can be described as *minimizing tradeoffs*, which can occur by producing (e.g., quinoa mono-cropping) (Jacobsen 2011) and consuming (e.g., toxic effects of cruciferous vegetables) too much of one single species (Lavecchia et al. 2013). Here we outline four broad factors underlying the profusion of (bio)diversity indices used in the scientific literature to test such hypotheses.

First and foremost, (dietary) diversity lacks a formal and unambiguous definition. It can and has been defined in many different ways, depending on which specific aspect (see Supplementary material, Figure S1) of this expansive and complex concept is of interest to the researchers involved (Verger et al. 2021; Daly, Baetens, and De Baets 2018). Consequently, candidate food biodiversity indices

measure demonstrably different "units" of diversity [e.g., species, food groups, or traits (e.g., nutrient density); see "Components of food biodiversity"] and no single index can serve as an all-encompassing summary statistic.

Second, the concept of diversity is often confounded with the indices that measure it. Verger, Dop, and Martin-Prével (2017) illustrate this issue within *nutrition* with the example of food group diversity: the 12-point Household Dietary Diversity Score (HDDS) is a proxy for a household's economic access to food (Swindale and Bilinsky 2006), but HDDS is often, invalidly, used as a proxy for an individual's dietary diversity. HDDS includes three food groups (oil and fats, sugar and honey, and miscellaneous) that are not included in other dietary diversity scores, because they do not provide essential micronutrients. Furthermore, food subgroups with distinct micronutrient profiles, such as dark green leafy vegetables, other vitamin A-rich fruits and vegetables, other vegetables, and other fruits are aggregated to the generic vegetables and fruits food groups (Supplementary material, Table S1). Moreover, dietary diversity is not merely a consequence of higher caloric or protein adequacy or household income, but also of the intra-household distribution of the food basket. Likewise, the most commonly used ecological diversity index in food supply studies, the Shannon index (Remans et al. 2014; Baye et al. 2019), is actually a measure of *entropy*. Entropy refers to the disorder or uncertainty in a system: it is more difficult to predict the identity of a randomly selected food commodity (in terms of e.g., species, zinc content) in a very diverse national food supply, whereas this prediction is less uncertain in a homogenous supply with only a few food types. Hence, the former food supply has a higher entropy than the latter. Entropy therefore shares important conceptual similarities with diversity. Although entropy measures are rational and frequently used indices of food system or dietary (bio)diversity, this of course does not imply that entropy is equivalent to diversity.

Third, dietary indices typically aim to condense all relevant information about an individual's or group's [e.g., Minimum Dietary Diversity for Women (MDD-W)] (Food and Agriculture Organization of the United Nations 2021) dietary pattern into a single real number (Miller et al. 2020). Hence, there are immeasurably many ways of calculating a food diversity index and achieving a specific value of the derived score (e.g., intake of two animal *vs* plant source food groups) from the often extensive and complex food intake data (Hanley-Cook, Argaw et al. 2021). Dietary diversity indices can weigh different components of these data more heavily than others (e.g., relatively more vegetal food groups), and can even entirely overlook some (e.g., spices, edible insects, snails do not count toward MDD-W) (Food and Agriculture Organization of the United Nations 2021). Therefore, analogous to the various conceptual definitions of diversity mentioned above, the myriad possibilities for mathematically formulating a diversity index have led to a huge number of indices, each providing a different estimate of ostensibly the same quantity (Daly, Baetens, and De Baets 2018).

Lastly, there is considerable discrepancy regarding the concept of diversity across scientific disciplines (Daly, Baetens, and De Baets 2018). Transfer of indices from one

field to another, although often tantalizingly similar, often overlooks their fundamental, discipline-specific nuances (Drescher, Thiele, and Mensink 2007; Katanoda, Kim, and Matsumura 2006). To illustrate, a key conceptual difference often underlies (at-scale) assessments of *ecological* diversity and *dietary* diversity. The former take into account the actual abundances (e.g., frequency, biomass) of the different species present in an ecosystem (Daly, Baetens, and De Baets 2018), while the latter are instead more concerned with an abstract allocation of e.g., food and drink commodities to broad functional food groups (e.g., nuts and seeds) (Food and Agriculture Organization of the United Nations 2021). Conventional dietary diversity indices often apply minimum quantity thresholds (e.g., one tablespoon) for food groups or food items to "count" toward the total score (Hanley-Cook, Argaw, et al. 2020), rather than assessing the distribution (e.g., % kcal contribution) of individual species across a whole diet (Hanley-Cook, Kennedy, and Lachat 2019).

The purpose of an index's use and its nutritional (or biological) interpretation depends strongly on the context of the dietary intake study. Examples might include: classifying shifts in food biodiversity after a nutrition-sensitive policy change or intervention (e.g., participatory home-garden diversification) (Boedecker et al. 2019); ranking diets in terms of their (relative) biodiversity (Remans et al. 2011); detecting the effects of external (typically anthropogenic) factors on dietary diversity (Martin-Prevel et al. 2012); or understanding interactions or substitutions between diversity at different levels (e.g., how changes in *between* food group diversity might affect *within* food group diversity) (Schulze et al. 2018; Vandevijvere et al. 2010). For each of these goals and many others, some indices will be more suitable than others, and a misguided choice may lead to misleading or even false conclusions (see "Food biodiversity indices").

In this narrative review, we focus predominantly on edible *species* diversity since it is often the lowest level of taxonomic detail available from (quantitative) dietary assessments (Lachat et al. 2018) and national food supply data (Remans et al. 2014). Moreover, we aim to leverage the extensive body of relevant theoretical and practical knowledge that has already been established in ecology (Daly, Baetens, and De Baets 2018). Nonetheless, we acknowledge that at lower taxonomic levels there is also important nutritional heterogeneity (e.g., 10,000-fold differences in vitamin A levels between banana varieties and 23-fold differences in iron content between sweet potato varieties) (Burlingame, Charrondiere, et al. 2009; Berti and Jones 2013).

Components of food biodiversity

(Bio)diversity is generally divided into three synergistic components: richness, evenness, and disparity. In this section, we provide definitions of these three key dimensions, as illustrated in Figure 1, as well as a brief summary of their nutritional (and biological) significance.
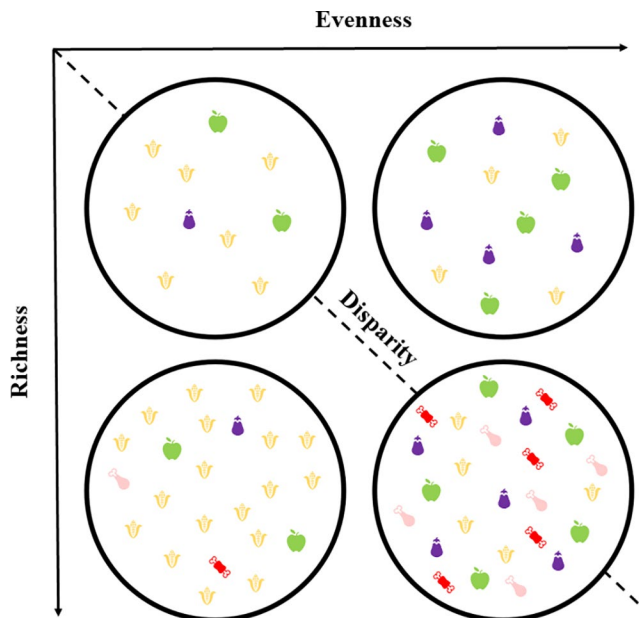
Figure 1. Partitioning food biodiversity in four dietary patterns. Distinct species are indicated by their color (i.e., yellow [*Zea mays* (maize)], green [*Malus domestica* (apple)], purple [*Solanum melongena* (aubergine)], red [*Bos taurus* (cow)], and pink [*Gallus gallus* (chicken)]). *Richness* (y-axis) is the absolute number of unique species: in e.g., the top left diet, it is equal to three, whereas in e.g., the bottom left diet, it is equal to five. *Evenness* (x-axis) is the equitability of the species abundance distribution (e.g., frequency, weight) in the diet: in e.g., the top right diet all species are present in an equal abundance and so it is perfectly even, while e.g., the bottom left diet is very uneven since it is dominated by maize. *Disparity* (z-axis) is the level of similarity between species in a diet: cow and apple (bottom right) are less similar to each other, e.g., nutritionally and taxonomically, than apples, maize, and aubergine. Adapted from Hanley-Cook et al. (2021).

Richness

The absolute number of species present in a diet or food supply is referred to as its *richness* or count (Lachat et al. 2018; Jones et al. 2018; Penafiel et al. 2019; Wertheim-Heck and Raneri 2019). The conceptual definition of richness is based on two assumptions.

First, that a classification of "units" exists and is known. Short of such a classification, it might be unclear to which taxon or food group any particular food item belongs, thereby complicating or precluding any richness calculation. The challenges of species taxonomy are well-known, e.g., previous ethnographic studies have misidentified between 2-10% of specimens (Łuczaj 2010). However, a unique *nutritional* challenge is that food and drink commodities often belong to diverse functional food groups (e.g., chicken meat and eggs), but are taxonomically (i.e., through the lens of *ecology*) regarded as identical species (i.e., *Gallus gallus*) (Hanley-Cook, Huybrechts, et al. 2021).

The second assumption is that each "unit" is equally distinct, so that no two species are more or less similar than any two other ones. However, this almost never holds in either nutrition or ecology; to illustrate, amaranth, quinoa, and spinach converge on the phylogenetic tree, but spinach has a diverging micronutrient profile. Hence, simple count measures [e.g., food item variety scores (Drewnowski et al. 1997)] often fail to distinguish whether the observed

diversity/richness is the result of healthy or unhealthy foods (e.g., fruits, red meat, refined grains) (Hanley-Cook, Huybrechts, et al. 2021) and assume simple linear additive effects of increasing total consumption (Schulze et al. 2018). Although food group diversity scores often circumvent this limitation by only counting certain foods (World Health Organization and UNICEF 2021; Food and Agriculture Organization of the United Nations 2021), such methods are normative (i.e., how to objectively categorize micronutrient fortified, sugar-sweetened wholegrain cereals?) (Drescher, Thiele, and Mensink 2007). Moreover, food group aggregation inherently leads to a substantial loss of data granularity i.e., *within* food group diversity is completely obscured for descriptive or association analysis (Hanley-Cook, Kennedy, and Lachat 2019).

From a statistical and quantitative perspective, richness is the most straightforward component of (food) biodiversity, being an enumeration of the different food species present in a diet or food supply. Of course, in practice researchers can only "count" those species collected in their data: no dietary pattern can be fully enumerated, due to the practical limitations of dietary assessment methods, such as recall or observer biases (Shim, Oh, and Kim 2014). Thus, species richness must be estimated from e.g., 24-hour recalls (Lachat et al. 2018) or (self-reported) food frequency questionnaires (Hanley-Cook, Huybrechts, et al. 2021) and hence estimates of absolute richness are likely to be strongly correlated with a study's population group, sample size, and enumeration time-frame and duration (Daly, Baetens, and De Baets 2018; Drewnowski et al. 1997; Jones 2017).

Evenness

Besides the total number of species in a diet, the relative distribution of their abundances, referred to as the diet's *evenness*, is also an important component of diversity (Vadiveloo et al. 2014). In ecology, a community is perfectly even if every species is present in equal proportions (e.g., frequency or biomass), and uneven if a small number of species dominate the abundance distribution (Daly, Baetens, and De Baets 2018). From a nutritional perspective, the latter assumption is not often desired, and might potentially be addressed by evidence-based weighting factors for food groups or individual species (Drescher, Thiele, and Mensink 2007). Indeed, according to food-based *moderation* recommendations, which combines aspects of *evenness* and functional *disparity* (see below), healthy foods should be consumed in higher proportions (e.g., g/day, kcal/day) than unhealthy ones (e.g., fruit and vegetables *vs* refined starchy staples) (Fischer and Garnett 2016; Herforth et al. 2019).

Unlike for species richness, there currently is no accord on how to measure evenness in *ecology* (Daly, Baetens, and De Baets 2018). In *nutrition*, an additional complicating factor is that neither a widely accepted global reference diet (e.g., to define the optimal (food group) abundance distribution, based on % kcal contributions) (Hanley-Cook,

Argaw, et al. 2021; Vaidyanathan 2021), nor efforts to quantify the optimal *within* food group species richness currently exist (Hanley-Cook, Huybrechts, et al. 2021; Bhupathiraju et al. 2013). The important role of species evenness (let alone moderation) in whole dietary patterns, has thus received less attention than that of edible species richness (Lachat et al. 2018).

In general, reviews on *ecological* diversity recommend that researchers choose an index most suited to their particular needs, given the lack of a universal way to measure evenness (Tuomisto 2012). However, attention should be paid to motivating the choice of food biodiversity indices by considering their mathematical behaviors and nutritional interpretations (see "Food biodiversity indices").

Disparity

Most *ecological* diversity indices account for two components of diversity – richness and evenness – and thus implicitly assume that distinct (food) species have nothing in common. In other words, they ignore any functional similarity (e.g., protein quality, cumulative energy demand) between species. This conception of diversity is referred to as *species-neutral* diversity. It implies, for instance, that a diet of five dramatically different species (e.g., maize, beans, squash, sweet potato, and tilapia) is considered to be no more diverse than a diet composed of five cereal species. In contrast, in *nutritional* epidemiology, functional disparity is the basis of *between* food group indices (Jones 2017; Remans et al. 2011), which aggregate individual food items based on their nutrient profiles (e.g., vitamin A content as a "trait") (Arimond et al. 2010; Food and Agriculture Organization of the United Nations 2021).

There are relatively few biodiversity indices capable of reflecting the more realistic and nuanced situation of dissimilarities between distinct edible species (Daly, Baetens, and De Baets 2018). These indices are termed *similarity-sensitive*. Classical indices, such as Dietary Species Richness (DSR) or Gini-Simpson index (see "Food biodiversity indices"), depend entirely on the notion of species as the functional "unit" (Hey 2001; Lachat et al. 2018), and are thus seriously affected by taxonomic reclassification (Daly, Baetens, and De Baets 2018). Likewise, a dietary diversity scores maximum and predictive ability for micronutrient adequacy is entirely dependent on the degree of food (sub)group aggregation (Martin-Prevel et al. 2017).

In *ecology*, various distance measures have been developed to (objectively) measure disparity between pairs of species (see "Food biodiversity indices"; Daly, Baetens, and De Baets 2018). When adopted in nutrition or food systems research, they generally associate with each focal food species some data concerning the characteristics deemed to be important, such as a list of functional "traits" (e.g., vitamin C, iron content) (Remans et al. 2011), morphology (e.g., liquid, solid), or location on a phylogenetic tree (e.g., plant, animal) (de Otto et al. 2015).

Food biodiversity indices

Axiomatic characterization of indices

Food (bio)diversity indices must synthesize and summarize high-dimensional dietary intake data, typically by mapping it to a scalar (e.g., food group scores, DSR, Gini-Simpson index). The formulation of a diversity index (e.g., the "unit" of aggregation, and inclusion or exclusion of actual quantities consumed) will affect how food biodiversity can be connected to its composition *within* and *between* food groups and its functionality (Hanley-Cook, Kennedy, and Lachat 2019). Therefore, to draw any nutritional or (biological) conclusion, it is essential for researchers to understand the fundamental assumptions underlying the mathematical formulation, known as *axioms*, of a particular diversity index.

For *ecological* indices an axiomatic basis was identified decades ago (Renyi 1961; Davydov and Weber 2016), allowing users to identify an index's most important properties and consequently to differentiate between diversity indices based on which axioms they do or do not satisfy. An extended mathematical description and discussion of these axioms can be found in a review by Daly, Baetens, and De Baets (2018). In general, the (non-exhaustive) axioms recapitulated in Table 1 are agreed upon to be desirable for *ecological* diversity indices (Daly, Baetens, and De Baets 2018), but are to our knowledge have neither been considered, nor integrated into seminal research on food biodiversity indices.

As briefly touched upon in "Conceptualizing food biodiversity," through a nutritional lens Axioms 3 and 4 are not warranted, as evidence-based distributions (e.g., kcal/d) across food groups diverge considerably. To illustrate, the EAT-*Lancet* Commission recommends fish intakes of ~40 kcal/day *vs* legume intakes of ~436 kcal/day (Willett et al. 2019). Nevertheless, if an index fails one of these axioms, this should be considered as a cautionary sign rather than a reason for dismissal, since the diversity index may still be useful in contexts where that axiom is less important. For example, Axiom 4 permits a (partial) ordering of diets based on their diversity. Hence, if an index fails to satisfy this axiom it should not be used to make a quantitative comparison of diets by their relative diversities, which is frequently (Hanley-Cook, Huybrechts, et al. 2021; Fung et al. 2018), but not always (Kuczmarski et al. 2019; Rawal et al. 2020), the goal of (observational) food intake studies.

Inventory of indices

In the remainder of "Food biodiversity indices" we provide an overview of the biodiversity indices that are most widely used in *ecology* and which have been applied more recently to dietary intake and food supply data. Following Daly, Baetens, and De Baets (2018), we classify these in two main groups: *classical* indices and *similarity-sensitive* indices.

Throughout, we consider a diet of S species, where p_i represents the proportional abundance of species i, so that $0 \leq p_i \leq 1$ and $\sum_{i=1}^{S} p_i = 1$. If the abundances are measured by e.g., counting non-composite or decomposed food items, then the relative abundance p_i represents the probability of randomly selecting a food item of species i from amongst all food items in the diet. If the abundances are measured in terms of e.g., kcal, then the relative abundance p_i represents the relative share of the whole diet's total energy that was stored in food items of species i.

Classical indices

Definitions. The input for the most widely used biodiversity indices is the vector of relative abundances $\mathbf{p} = (p_1, \ldots, p_S)$, where S is the total number of unique species in the diet (Katanoda, Kim, and Matsumura 2006). These indices measure species-neutral diversity (i.e., do no account for disparity; see "Components of food biodiversity") and are known as *classical diversity indices*.

Conceptually, the simplest biodiversity index of all, *richness* itself, has only recently been applied in food consumption studies with species level detail (Lachat et al. 2018; Hanley-Cook, Huybrechts, et al. 2021; Bernhardt and O'Connor 2021; Vogliano et al. 2021):

$$H_{SR}(\mathbf{p}) = S \qquad (1)$$

DSR, or a count of the unique number of edible species in a diet, has been associated with higher micronutrient adequacy among groups of women and children in seven low- and middle income countries (Lachat et al. 2018; Penafiel et al. 2019). Lachat et al. (2018) also reported that the highest micronutrient adequacies were obtained when both DSR and food group diversity (~nutritional dissimilarity) were high. Furthermore, DSR was inversely correlated with body fat percentage and positively related to the use of wild and cultivated foods among women in the Solomon

Table 1. Most commonly assumed axioms that an ecological diversity indicator $H(p)$ should satisfy.

1. Symmetry	$H(p_1, \ldots, p_S)$ must be a symmetric function.
2. Continuity	$H(p_1, \ldots, p_S)$ must be a continuous function.
3. Evenness	The diversity measure is maximal for a fixed number of species S when all species abundances are equal.
4. Principle of transfers	A transfer of species abundance must increase diversity.
5. Monotonicity in number of species	The introduction of a new species must increase diversity.
6. Replication principle	The diversity of a pooled sample of n maximally distinct (i.e., no shared species) and equally diverse sub-groups is n times the diversity of a single sub-group.

For further reading see Hill (1973), Patil and Taillie (1982), Jost (2009), and Daly, Baetens, and De Baets (2018).

Islands (Vogliano et al. 2021). More recently, habitual DSR was associated with significantly reduced rates of mortality among ~450,000 European adults (Hanley-Cook, Huybrechts, et al. 2021). Traditional food species richness (i.e., locally hunted, gathered, cultivated, or raised) was also related with greater usual protein, fiber, vitamin, and mineral intakes among mothers and children in Peru (Roche et al. 2008). Moreover, DSR of aquatic species enhanced micronutrient and essential fatty acid provisioning, independent of total seafood consumption quantity (i.e., simulated diets achieved more nutrient targets per 100 g of tissue) (Bernhardt and O'Connor 2021). Da Silva and Begossi (2009) assessed an Amazonian population's dietary richness of animal protein sources by counting the number of unique animal species, as recalled by individuals and from the direct observation of food consumption in households. Following guidance by the Food and Agriculture Organization of the United Nations and Bioversity International (2017), Ntwenya et al. (2017) constructed the Food Biodiversity Score by summing the various edible parts (e.g., spinach leaves or stems) or stages of maturity of the same food species (e.g., ripe or unripe mango) consumed by a household member the previous day or night, which indicated that Tanzanian diets were non-diverse, despite a rich local biodiversity.

In nutritional epidemiology, the concept of dietary *richness* has been widely applied beyond the species level. To illustrate, de Otto et al. (2015) defined richness as the number of distinct food and beverage items consumed more than once per week. Likewise, Chegere and Stage (2020) constructed a household richness score, which was simply an absolute count of the number of food items (~food variety) consumed by anyone in a household over a seven-day period. Salomé et al. (2020) characterized *count* as the number of unique food subgroups consumed (~food group diversity). Rawal et al. (2020) and Kuczmarski et al. (2019) calculated richness based on the habitual consumption of at least half a cup or ounce equivalent from 21 (healthful) food groups. In Bangladesh, Kennedy et al. (2005) enumerated the number and frequency of distinct cultivars or varieties within a given species (e.g., rice, potato, banana) consumed by a household over a 24-hour period. Vandevijvere et al. (2010) expressed within-food group diversity as a simple count of the number of different food items consumed during the preceding day within each pre-defined food group. Khoury et al. (2014) quantified the species richness of national per capita food supplies in a given year as a count of present crop commodities on FAOSTAT.

However, richness is a poor estimate of diversity, because it takes no account of the food abundance distribution (i.e., evenness, or preferably moderation; see "Components of food biodiversity"). By omitting a key component of diversity, e.g., DSR takes the rudimentary and nutritionally unintuitive approach of assigning exceptionally rare/trivial edible species (e.g., kcal/day from saffron or ginger) equal weight as exceptionally common species (e.g., kcal/day from rice or potato).

The *Berger–Parker diversity index* considers the opposite extreme, and ignores all species, save the most dominant. It is defined as the reciprocal of the relative abundance of the most common species:

$$HBP(\mathbf{p}) = \frac{1}{max_i\, p_i} \qquad (2)$$

and thus estimates the relative dominance of this species as a proxy for the biodiversity of an entire diet or food system. In this spirit, Khoury et al. (2014) quantified *species dominance* as the proportion of a country's per capita food supply comprised of the most abundant (e.g., kcal/capita/day) crop commodity.

The *Shannon diversity index*, also known as the Shannon-Wiener index, and the Shannon entropy, provides a more balanced estimate of diversity by including all species in its calculation. It measures the uncertainty in the outcome of a sampling process (Shannon 1948), and is given by:

$$HSh(p) = -\sum_{i=1}^{S} p_i ln\left(p_i\right). \qquad (3)$$

Remans et al. (2014) and Nelson et al. (2018) used the Shannon index to assess how many different types of food items were available in a country's food supply, and how evenly these different types were distributed/consumed by gram per capita per day. Furthermore, Béné et al. (2020) assessed food systems' biodiversity at country level by quantifying crops' calorie diversity using the Shannon index. Baye et al. (2019) converted national agricultural production data to seven food groups and used the Shannon index to assess changes in production diversity in Ethiopia (i.e., p_i is the proportion of the total production coming from food group i). Gustafson et al. (2016) and Chaudhary, Gustafson, and Mathys (2018) used the Shannon index to assess the diversity of food items in a given country as a proxy of nutrient adequacy of food supplies, where p_i is the share (by weight) of food item i in the food system. Food production diversity was also estimated with p_i representing the shares of agricultural production for the country, again by weight of each food produced (Gustafson et al. 2016; Chaudhary, Gustafson, and Mathys 2018). Of note is that the Shannon index is more biased toward evenness than richness (i.e., gives more significance to common species).

Tian et al. (2017) aimed to assess the distribution of usual food intakes (i.e., from 3 consecutive 24 hour recalls) across six food groups. Entropy was represented as a function of the consumption share w_i, with:

$$H = \sum_{i}^{n} w_i ln\left(\frac{1}{w_i}\right). \qquad (4)$$

Here, entropy is maximized when consumption shares are equally distributed among different food groups (i.e. $w_i = \left(\frac{1}{n}\right)$ for all i) and food groups consumed in a greater quantity have a larger weight in the index.

The Shannon index is also the basis of *Pielou's evenness index*, which is given by:

$$J = \frac{H_{Sh}}{H_{Sh}^{*}}, \qquad (5)$$

where H_{Sh}^* is the maximum value of H_{Sh} (a function of S). It is the most widely used evenness index in the ecological literature, despite being an exceptionally poor estimate of evenness given its strong dependence on species richness (Daly, Baetens, and De Baets 2018). Khoury et al. (2014) assessed the evenness of calories, protein, fat, and weight in contributing crop commodities to national food supplies using Pielou's evenness index, but acknowledged the aforementioned limitation and consequently also assessed species dominance (see above).

The *Simpson diversity index* represents the probability that two ingredients taken at random from a diet (with replacement) represent the same species (Keylock 2005). As originally proposed by Simpson, it is given by:

$$H_{Si}(\mathbf{p}) = \sum_{i=1}^{S} p_i^2 .$$ (6)

Note that this formulation implies that lower values of the index indicate higher diversity. To avoid this counterintuitive behavior, two other formulations of this index are more commonly used. The *Gini-Simpson diversity index*, also called the Berry index represents the probability that the two (non-composite) food items represent different species, and is thus the complement of Simpson's original formulation:

$$H_{GS}(p) = 1 - H_{Si}(p).$$ (7)

To illustrate, Borkotoky, Unisa, and Gupta (2018) applied both the Simpson index to quantify the diversity of household level food group consumption and the Gini-Simpson diversity index to quantify the state level diversity of expenditure on different food groups over a one-month period. Furthermore, Katanoda, Kim, and Matsumura (2006) and Otsuka et al. (2016, 2017) applied a modified Gini-Simpson diversity index; coined as the Quantitative Index for Dietary Diversity (QUANTIDD), to national dietary survey data in Japan:

$$\text{QUANTIDD} = \frac{1 - \sum_i^n p_i^2}{1 - \frac{1}{n}},$$ (8)

with p_i defined as the proportion of total energy or nutrient intake originating from food group i and n being the total number of food groups. Thus, a maximum value is obtained when all food intake sources are equally distributed over the food groups. Similarly, de Otto et al. (2015) calculated the Berry index for participants in a multi-ethnic American cohort, based on the relative intake distribution of calories across individual food and drink items. Lachat et al. (2018) used the Gini-Simpson diversity index to quantify the number of different species in a diet and how evenly the consumed quantities (g/day) were distributed. Salomé et al. (2020) used the Berry index to assess the evenness of energy or protein intake among food groups, where p_i was the share of food group i in the total amount of energy, protein, or plant-protein intake, and n was the total number of food groups. In addition, the authors applied the Simpson index to assess the contributions of plant-based and animal-based food families to overall plant and animal protein intakes, respectively (Salomé et al. 2021).

However, Drescher, Thiele, and Mensink (2007) argue that the maximum value of a dietary diversity index should be assigned to individuals who consume recommended food (sub)group shares. Therefore, the authors modified the Gini-Simpson diversity index by incorporating a health value based on the share of food weight and a subjective understanding of the food guidelines of the German Nutrition Society. Likewise, Vadiveloo et al. (2015, 2014) evaluated dietary evenness by adjusting the Gini-Simpson diversity index by a health value based on the share of food volume (i.e., cups) and the authors' interpretation of the Dietary Guidelines for Americans 2010-2015. Furthermore, Rawal et al. (2020) and Kuczmarski et al. (2019) followed a similar approach, where p_i is the share of food item i in the total energy intake and n is the total number of food items consumed, but they corrected for a health value based on the more recent Dietary Guidelines for Americans 2015-2020. Wang et al. (2021) recently used the Gini-Simpson index to represent the probability that two randomly chosen commodities of an individual's food profile (with replacement) belonged to two different food items. At present, guidance on the optimal composition of intra-food group species richness and the recommended consumption shares (e.g. % energy or volume) of individual food species are absent.

The *Simpson dominance index* gives more weight to common species than to rare species. It is the reciprocal of Simpson's original formulation and is given by:

$$H_{SD}(\mathbf{p}) = \frac{1}{H_{Si}(\mathbf{p})}$$ (9)

In the literature, 'Simpson index' has been used interchangeably for all three of the formulations described above (Daly, Baetens, and De Baets 2018). This confusion could be avoided by researchers clarifying specifically which form of the index they employ.

The Simpson index is also occasionally (mis)used as a measure of evenness, which is not appropriate since it also varies with richness. Instead, the richness effect should first be eliminated by dividing the index by its maximum value, which depends on S or n (Daly, Baetens, and De Baets 2018).

Drawbacks of classical indices. At present, the most widely applied measures of food biodiversity are DSR, the Shannon index, and the (weighted) Gini-Simpson index. They are excellent examples of the key limitations associated with classical indices (see "Conceptualizing food biodiversity" and "Components of food biodiversity"). These issues fall into two categories: i. direct comparisons between diets (or food supplies) using different indices,

and ii. comparisons between diets using the same index.

In the first case, we are faced with the reality that each of these diversity indices measures fundamentally different features of a diet, and therefore has a different unit. DSR is the number of distinct edible species in a diet, the Simpson index represents the probability that two randomly selected (non-composite) food items belong to the same species, and the Shannon index is a measure of the entropy or disorder of the diet. Richness is measured in units of taxa (i.e., species), the Simpson index is a probability, and the Shannon index is an entropy measure, with the unit of bits of information. Thus, to avoid misinterpretation of their absolute values, biodiversity measurements obtained using different classical indices should not be blindly compared across (or within) studies (Daly, Baetens, and De Baets 2018).

To illustrate the second case, let us consider the simplest possible example: a diet composed of S equally-common species. Disregarding dietary moderation recommendations for ease, it seems reasonable to say that a diet D_1 with ten equally-common species is twice as diverse as a diet D_2 with five equally-common species. But calculating, for example, the Shannon entropy, we find $H_{Sh}(\mathbf{p}_1) = 2.30$ for the first diet and $H_{Sh}(\mathbf{p}_2) = 1.61$ for the second. It is not clear how we should understand the difference in biodiversity between these two diets. The diversity of the first diet is not twice that of the second, although our intuition tells us otherwise. It is additionally unclear what these values might mean in absolute terms: should we consider a diversity of 2.3 to be high or low? Without an intuitive unit, we hesitate to draw clear conclusions.

Non-linearity is another issue affecting classical indices, which can in some cases significantly affect their suitability for food biodiversity analysis. For example, if an individual's perfectly even (e.g., kcal/species/d) dietary pattern consisting of 100 species is confronted with some nutrition disaster (e.g. humanitarian crisis) that renders all but 10 usually consumed species available, the Gini-Simpson index of this community will drop from 0.99 to 0.90. So despite the fact that more than 90% of the species of the pre-catastrophe diet have been removed, the Gini-Simpson diversity index only drops by 9%. Monitoring and evaluation of e.g., drought, crop failure, and famine using this index would probably conclude that this individual's food biodiversity was not greatly affected, while the opposite is true. The same issue affects the Shannon index, but to a lesser degree (Daly, Baetens, and De Baets 2018). Clearly, the selection and interpretation of (bio)diversity indices should be guided by the research question at hand.

Many scientists have ignored the consequences of these issues. In their view, the absolute values of the indices are unimportant, as long as they can be used to calculate the statistical significance of the change in biodiversity following a disturbance (Jost 2009) or associations across levels with a diet-related outcome (Remans et al. 2014; Hanley-Cook, Huybrechts, et al. 2021). Yet, in many cases this is not a reasonable basis for study conclusions, since the statistical significance of a change in a food biodiversity index often has little to do with the actual magnitude or physiological/

clinical significance (Martin-Prevel et al. 2012). For the same reason, one index may indicate a statistically significant change in diversity while another (complementary) index does not (de Otto et al. 2015).

Similarity-sensitive indices

The third component of diversity, disparity (see "Components of food biodiversity"), is absent from classical biodiversity indices. This omission can be remedied by reformulating these indices to include a similarity measure.

Similarity-sensitive indices incorporate a similarity matrix encoding pairwise species similarities, which becomes an additional input of the index along with the species abundance vector. For e.g., a country's food supply of S species, an $S \times S$ matrix $Z = (Z_{ij})$ is constructed, where Z_{ij} is a measure of the similarity between species i and j.

Bernhardt and O'Connor (2021) indicated positive relationships in functional nutritional traits of seafood species (i.e., concentrations of micronutrients and fatty acids relative to Recommended Daily Allowances) by ecological functional diversity, such as their habitat, trophic position, body size, diet source, and feeding mode. DeClerck et al. (2011) illustrated nutritional functional diversity (NFD) of edible plants in Kenya by classifying species according to the content of seven key nutrients. The identified species (e.g., high in protein, carbohydrates, or micronutrients) were then represented as a branch length from a dendrogram. NFD thus reflects the similarity in nutrient compositions within a cropping system (Bogard et al. 2018). To estimate disparity between food items, de Otto et al. (2015) used the *Jaccard distance* (Real and Vargas 1996), a measure of the diversity of the attributes of foods consumed, based on 12 food traits related to cardio-metabolic health (e.g., trans-fat content, glycemic load). In the same way, Salomé et al. (2020) assessed the extent to which food items differed nutritionally, based on nutrient composition (i.e., cutoff was above or below the median composition of a nutrient for all food items consumed among study participants). The Jaccard distance between two food items i and j is defined as:

$$J_{ij} = \frac{B_i + C_j}{A_{ij} + B_i + C_j}, \tag{10}$$

where A_{ij} is the number of attributes shared by food items i and j, B_i the number of attributes unique to i, and C_j the number of attributes unique to j. Wang et al. (2021) used the weighted Jaccard index to quantify the nutritional similarity between food items i and j:

$$J_{ij} = 1 - \frac{\sum_a min(G_{ia}, G_{ja})}{\sum_a max(G_{ia}, G_{ja})}, \tag{11}$$

where G_{ia} represents the weight of nutrient a in food item i; $J_{ij} = 0$ indicates that food item i and food item j share exactly the same nutrient constituents, while $J_{ij} = 1$ means they have totally different constituents.

Similarly, Rawal et al. (2020) and Kuczmarski et al. (2019) constructed a pairwise similarity score based on the presence or absence of 10 nutritional traits relevant to cardiovascular health (e.g., whole grain, fiber, alcohol). To estimate disparity, the *Mahalanobis distance*, which accounts for correlations between traits, thus eliminating double-counting, was used to derive the diversity of attributes of individual food consumption. It is given by:

$$Mij = \sqrt{\left(x_i - y_i\right)^T \Sigma^{-1} \left(x_i - y_i\right)}, \qquad (12)$$

where x_i is the vector of trait values for food i, y_i is the vector of trait values for food j, and Σ is the variance-covariance matrix among the attributes. The authors acknowledge that varying distance measures, along with the number of and arbitrary cutoff criteria for attributes, hamper the comparability of dissimilarity indices across available food intake studies (Rawal et al. 2020).

Remans et al. (2014, 2011), Gustafson et al. (2016) and Chaudhary, Gustafson, and Mathys (2018) measured modified functional attributable diversity (MFAD) of national food supplies, which is defined as "the sum of the pairwise functional dissimilarities of a collection of species measuring the dispersion of species within a functional trait space" (i.e., the diversity of nutrients provided by different food items based on the nutritional composition and the amount of each food item present). The modified approach to NFD meets two essential criteria: that functional diversity should not increase with functionally identical species, but should increase with functionally dissimilar species. It is represented as:

$$\text{MFAD} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} d_{ij}}{n}, \qquad (13)$$

where n is the number of edible species (or food items) and d_{ij} is the dissimilarity between species i and j as defined by nutritional components or traits measured using a distance function, such as the Euclidean distance measure:

$$d_{ij} = E_{ij} = \sqrt{\left(i_1 - j_1\right)^2 + \left(i_2 - j_2\right)^2 + \ldots + \left(i_n - j_n\right)^2} \quad (14)$$

where d_{ij} is the distance between food i and food j, i_1 is e.g., mg of iron in food i and j_1 is mg of iron in food j (Luckett et al. 2015), and n is the number of functional units, such that different foods that are identical in their trait composition are considered the same functional unit (i.e., redundant species not counted twice). Hence, it is possible that e.g., the Shannon entropy is high, but MFAD low when a large number of nutritionally similar staple crops (e.g., maize, rice, teff) are produced or consumed thereby adding species richness and/or evenness, but no functional diversity through a nutrition lens (Remans et al. 2014). As briefly discussed above, potential limitations (or strengths depending on the research objective) of trait-based approaches are the arbitrary number and varying selection criteria of traits themselves (i.e., health-related, agro-ecological traits, or both). Moreover, if variations in nutrient contents of food species are used as similarity criteria, we must acknowledge that only a fraction of edible species have (detailed) food composition data available (Charrondière et al. 2013).

Remans et al. (2011) reported that MFAD, computed from plant's macronutrient, mineral, and vitamin contents, was able to summarize nutritional diversity (i.e., variability) across farms and villages, but did not find a relationship between farm level MFAD and household dietary diversity. Luckett et al. (2015) were the first to apply MFAD, based on energy and 17 nutrient contents, to food consumption data, within the framework of measuring the contribution of market purchases or home production to a household's dietary diversity. More recently, Lachat et al. (2018) computed MFAD based on 6 micronutrients for 234 species in whole dietary patterns of individuals, with the total branch length of the dendrogram reflecting the diversity in nutrient composition of the species consumed. At the population group level, dietary MFAD was linked to higher dietary micronutrient adequacy (Lachat et al. 2018), whereas at the national scale, food supply MFAD was associated with lower incidence of under-five child malnutrition (Remans et al. 2014).

Khoury et al. (2014) quantified between country similarity (i.e., β diversity; see Supplementary material, Figure S1 for a dietary intake analogy) in energy supply (kcal) from crop commodity composition over time as the Bray-Curtis (BC) distance to the global mean commodity composition, inclusive of abundance:

$$BCij = 1 - \frac{2C_{ij}}{S_i + S_j}, \qquad (15)$$

where C_{ij} is the sum of the lesser energy values for only those commodities in common between countries and S_i and S_j are the total number of crops counted in both countries, separately. Likewise, Wang et al. (2021). quantified the variations of food intake or nutritional profiles across different time points and individuals using Bray-Curtis distance.

A classic example of an ecological similarity-sensitive diversity index is *Rao's quadratic diversity index*, which is often called Rao's quadratic entropy although it is in fact not an entropy measure. It is defined as the expected similarity between two food items selected at random from the diet (with replacement) (Rao 1982), and is given by:

$$H_R(\mathbf{p}) = \sum_{i,j=1}^{S} d_{ij} p_i p_j, \qquad (16)$$

where d_{ij} is the similarity between species i and j. Note that H_R reduces to the Gini-Simpson diversity index in the case where $d_{ij} = 1$ for all $i \neq j$, and $d_{ii} = 0$ for all i.

Green et al. (2021) and Nelson et al. (2018) used Rao's quadratic index, based on a similarity matrix of nutrients weighted by the relative quantity of each food item, to calculate the nutrient diversity of food supplies. S is thus the total food item richness, p_i and p_j are the relative abundances of food items i and j; respectively, and d_{ij} the dissimilarity between foods i and j measured by differences in nutritional composition via the Euclidean distance measure [see Eq. (14)]. Likewise, Wang et al. (2021) computed the mean nutritional similarity between any two randomly selected food items in the diet recall using Rao's quadratic entropy.

Conclusions

Food biodiversity has been defined as "the diversity of plants, animals and other organisms used for food, covering the genetic resources *within* species, *between* species and provided by ecosystems" (Food and Agriculture Organization of the United Nations and Bioversity International 2017). However, there is a need for standardized and reliable indices to help define how to best measure and monitor food biodiversity and help quantify which aspects of diversity may maximize benefits to human nutrition and environmental sustainability. The lack of unified principles [e.g., species abundance unit (kcal, weight, volume), *between* and *within* food group weighting factors, functional traits] makes objective comparisons across different studies, population groups, or time points challenging. In this narrative review, we have provided an overview of the key conceptual issues researchers are confronted with when they seek to appraise food biodiversity, and we have surveyed and compared the most common ecological diversity indices used in dietary intake and food supply studies. In general, we recommend that food biodiversity indices are selected that:

i. satisfy the key axioms in "Food biodiversity indices," to ensure appropriate performance;
ii. can be extended to account for dissimilarity between edible species; and
iii. are used in combination, rather than interpreted in isolation, to exploit their complementarity (see e.g., country level (sub-)indices applied in the Agrobiodiversity Index) (Jones et al. 2021).

In the present paper, we have elaborated on each recommendation by motivating its importance for reasonable and realistic biodiversity measurement in diets (and foods systems). However, depending on the objectives (or the theory of change hypothesis) of a nutrition-related study, other dietary diversity indices may be more appropriate (e.g., MDD-W to monitor national food group consumption trends) or feasible (e.g., capturing neglected, underutilized, or wild species consumption often requires ethnobotanical or zoological expertise). As discussed in "Conceptualizing food biodiversity," the vast number and variety of available diversity indices allows researchers to be flexible in their choice of indices, with the key stipulation that the underlying definition of the index should first be considered carefully to ensure that it is appropriate for the particular application, and will not lead to misinterpretations. Food (bio)diversity/variety indices provide a summary of an inherently complex and multidimensional concept: a diet's or food supplies' (correlated) structure. Indices achieve this summarization in different ways by emphasizing different aspects of diversity, often in subjective manners. To avoid confusion and misinterpretation, users should first define their objectives and then choose the appropriate measure for the specific problem. Using a combination of ecological (and dietary) diversity indices is often warranted as they can capture unique aspects of nutritional quality (Bogard et al. 2018).

To avoid some of the limitations (e.g., non-linearity) and subsequent misinterpretation of classical indices, conversion of food intake data to *effective numbers* might be explored in nutritional epidemiology. In brief, to translate a diet to its effective number equivalent means to find an equivalent diet (i.e., same value of the index as the initial diet in question) that is perfectly even (Jost 2006). The use of effective number indices, which are always measured in units of number of *effective species* to assess changes in food biodiversity might allow for well-founded comparisons between different studies and even different indices (Daly, Baetens, and De Baets 2018). Even so, without evidence-based *moderation* weighting factors for food groups, or preferably individual edible species, effective numbers would remain nutritionally challenging to interpret (see "Components of food biodiversity" and "Food biodiversity indices").

To conclude, researchers and policy makers must give careful consideration to the selection of (valid) food biodiversity indices to assess the effectiveness of nutrition-sensitive programs, food trade and conservation policies, transportation infrastructure, and commodity market regulation on edible species diversity in food systems and subsequent human diets. Commitments such as the United Nations' Decade of Action on Nutrition (2016-2025) and Decade of Ecosystem Restoration (2021-2030) provide global and national stimuli for cross-cutting and holistic initiatives on nutrition and biodiversity conservation.

Competing interests

The authors have declared that no competing interests exist.

IARC disclaimer

Where authors are identified as personnel of the International Agency for Research on Cancer/World Health Organization, the authors alone are responsible for the views expressed in this article and they do not necessarily represent the decisions, policy or views of the International Agency for Research on Cancer/World Health Organization.

Funding

Abbreviations

DSR	dietary species richness
HDDS	Household Dietary Diversity Score
MDD-W	Minimum Dietary Diversity for Women
MFAD	modified functional attributable diversity
NFD	nutritional functional diversity
SDG	sustainable development goals

ORCID

Giles T. Hanley-Cook http://orcid.org/0000-0001-9907-594X
Aisling J. Daly http://orcid.org/0000-0002-3390-2495
Roseline Remans http://orcid.org/0000-0003-3659-8529
Andrew D. Jones Jones http://orcid.org/0000-0002-9265-3935
Kris A. Murray http://orcid.org/0000-0002-8382-0674
Inge Huybrechts http://orcid.org/0000-0003-3838-855X
Bernard De Baets http://orcid.org/0000-0002-3876-620X
Carl Lachat http://orcid.org/0000-0002-1389-8855

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