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Review Paper

The flexible application of carrying capacity in ecology

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A B S T R A C T

Carrying capacity encompasses a broad collection of approaches used to better understand biotic interactions in ecosystems and is often applied with no explicit regard to its historical origin. In this paper, we reviewed the primary literature to examine how carrying capacity is applied in ecology. We focused our review on ecosystem studies—studies that frame their results at the ecosystem level—published after the 1950s and highlight emerging trends of this concept. We found that while carrying capacity offers some underlying commonalities, a wide range of definitions and approaches hinders a unified framework to better understand biotic ecosystem interactions. Not surprisingly, these studies most often use K—the number of individuals that the environment “can support” in a given area—to define carrying capacity, despite considerable ambiguity and uncertainty in this approach. Furthermore, the studies that we reviewed spanned several levels of ecological organization: molecules to communities and up to landscapes. To add further complexity, it is not clear whether carrying capacity was intended as a dynamic concept subject to temporal variability as it was often applied in the reviewed studies. We found that carrying capacity is most often applied to studies in conservation biology, rangeland and wildlife management, aquaculture, and fisheries biology. We explore ecosystem level responses to implications of “carrying capacity” overshoot and discuss proposed mechanisms that govern ecosystem carrying capacity. We discuss the usefulness of the concept and end with suggestions to improve carrying capacity's general application in ecosystem studies.

1. Introduction

Carrying capacity is a widely and commonly used concept among biologists to better understand biotic interactions with and within a system, independent of the level of system organization (Monte-Luna et al., 2004). The evolution of the carrying capacity concept is convoluted. Though carrying capacity is often attributed to the K variable in the logistic function from Verhulst (Verhulst (1838); Equation (1))—a model for population growth—Verhulst never employs the term "carrying capacity" (Sayre, 2008). The first use of Equation (1) in ecological applications has been attributed to both Lotka (1925) and Pearl and Reed (1920). Equation (1) shows that the population size at a time t is dependent on: r the intrinsic rate of growth, N the number of individuals, and K, historically referred to as the upper limit of growth.

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$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) \tag{1}$$

Nevertheless, carrying capacity has been extensively applied in a wide scale of studies, partially for its theoretical simplicity and widespread familiarity within the biological research community. Because of its broad theoretical appeal and potentially powerful applications in ecosystem management, it has been applied to a wide range of studies across scales. For example, at the molecular or cellular level, carrying capacity has been applied to: 1) studies that model the number of microbes in the phyllosphere (Remus-Emsermann et al., 2012); 2) understand the influence of earthworms on the soil microbial community (Groffman et al., 2015); and 3) link animal anatomy and physiology with hemoglobin oxygen carrying capacity (Dabruzzi and Bennett, 2014; De Domenico et al., 2013; Tufts et al., 2013).

Despite its wide application today, most of the contemporary studies that use carrying capacity are unaware of its genesis and historical application; in fact, the original application of carrying capacity is completely outside of the realm of biology. In the comprehensive review of the subject, Sayre (2008) discusses carrying capacity as it was originally defined and applied; carrying capacity was first applied in a mechanical engineering context to calculate the mass of a load that a steam ship could carry (Fig. 1a). Now, engineers use the term "payload" to describe the "carrying capacity" or load that a physical object could transport.

Carrying capacity was first applied to biological systems in the 1870s, however, it retained its literal application; in this use, it referred to the mass of meat that pack animals could physically transport (Fig. 1a). Sayre (2008) attributes the evolution of carrying capacity from a literal and quantitative concept to a figurative and qualitative concept from its application to livestock populations "being carried by the land where they lived" in the 1880s (Thomson, 1887). From this moment on, carrying capacity referred to a quasi-quantitative amount of something that could be "carried by the environment." The contemporary usage of carrying capacity was further shaped in the 1950s from the logistic curve originally developed over 100 years prior (Verhulst, 1838). In fact, it was not until the first edition of *Fundamentals of Ecology* when Odum (1953) assigned the term "carrying capacity" to the asymptote of the logistic curve, though there was very little empirical evidence of such a thing (Sayre, 2008). Before, according to Sayre (2008), the asymptote of the logistic curve was "simply an upper limit of growth." This new development undoubtedly influenced a generation of biologists, particularly at the population level of ecology—though there is considerable interest at several levels of ecological organization—and continues to be widely applied in the literature. This conceptual evolution of carrying capacity developed independently from the human carrying capacity approach (see Vogt, 1948) that is commonly used in the sustainability and development literature, despite sharing a common conceptual ancestor (Fig. 1a). In this study we focus on the former application of carrying capacity—the application more commonly associated with understanding biotic interactions in ecosystems that is independent of social implications—in the context of intrinsic limits of populations in ecosystem studies.

Though there are benefits of using a widely applied and familiar conceptual approach to studying populations and ecosystems, there are several limitations. For example, as discussed by Sayre (2008), carrying capacity (K) has never been empirically shown in the field, "distinguishing between organisms and environment as factors determining population growth was rendered intractable by the variability of environment itself." Furthermore, there are theoretical issues raised by

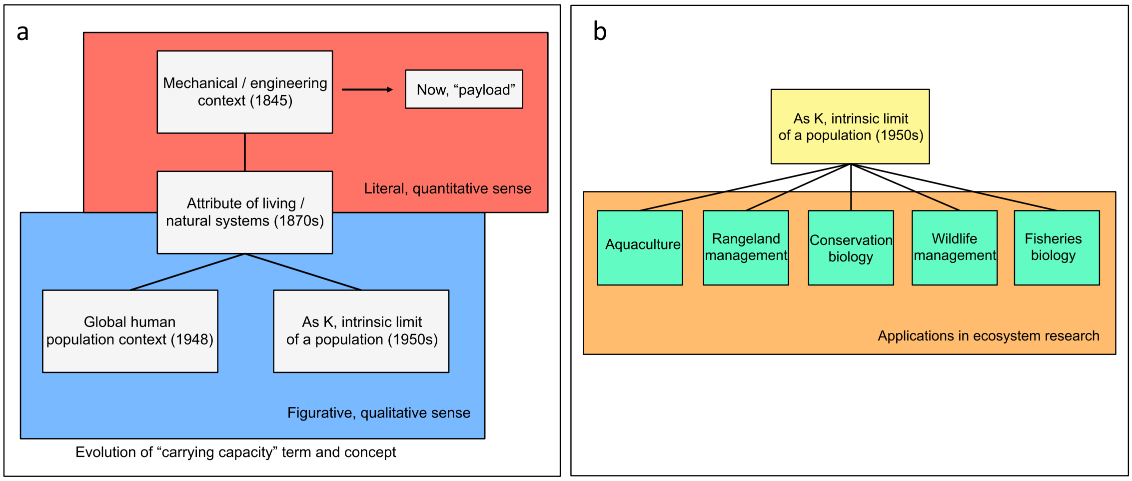

Fig. 1. (a) Conceptual timeline of "carrying capacity" in the literature. "Carrying capacity" originated in the mechanical and engineering context. This review focused on the application of carrying capacity approach as K, the intrinsic limit of a population. At some point in the late 19th century, carrying capacity evolved from a quantitative literal concept to a qualitative figurative concept. Payload is defined as a load that a physical object could transport. (b) After carrying capacity was assigned to the asymptote of the Verhulst (1838) equation in the 1950s, carrying capacity was widely applied in 5 different fields of ecosystems research. Carrying capacity has been extensively applied in aquaculture, rangeland management, conservation biology, wildlife management, and fisheries biology.

the idea of a dynamic carrying capacity; as Sayre (2008) concludes: "if carrying capacity is conceived as static, it is theoretically elegant but empirically vacuous; but if it is conceived as variable, it is theoretically incoherent or at best question-begging." For decades, carrying capacity has been applied to ecology studies—mostly at the population level—with very little attention to the historical origins or the conceptual flaws in the approach.

Despite these weaknesses, carrying capacity continues to be an important construct for many ecological studies. In this study we review how ecosystem studies—in the years following the assertion by Odum (1953) that the asymptote of the logistic curve is an environmental "carrying capacity"—use and define the carrying capacity concept, what governs ecosystem "carrying capacity," and what are the implications of overshooting the "carrying capacity" of an ecosystem. The aim of this study was not to diminish or discredit ecosystem studies using carrying capacity. Instead, we sought to provide an overview of ecosystem studies in the literature that use a carrying capacity framework to highlight specific commonalities within this broad and often ambiguous approach. By doing so, we focus on fundamental ecological themes and principles that are often missing from carrying capacity studies.

As much as carrying capacity provides an important theoretical lens to investigate biotic interactions with and within an ecosystem, this concept raises many difficult to answer questions. For example, how is carrying capacity used in ecosystem studies in the literature? More specifically: what information does the carrying capacity framework provide about an ecosystem and biotic and abiotic interactions within an ecosystem? In this paper we ask the following questions: 1) is there a unified approach to ecosystem studies using a carrying capacity framework; or more specifically; 2) what particular and fundamental ecological concepts, principles, and metrics are tested, used, or applied in ecosystem studies that use carrying capacity; and finally, 3) what are the mechanisms governing ecosystem carrying capacity? To answer these questions and to highlight fundamental ecological principles often masked by the carrying capacity label, we conducted targeted keyword searches in a peer-reviewed literature database and reviewed ecosystem studies that apply the carrying capacity framework.

2. Methods

To investigate how carrying capacity is applied to ecosystem studies in the literature, we conducted targeted keyword searches in Scopus, a large database of peer-reviewed literature. We focused our initial search on papers published after 1953 through 2016. In 1953, Odum assigned the term "carrying capacity" to the asymptote (Odum, 1953)—up until then referred to as "an upper limit of growth"—of the logistic equation developed by Verhulst (1838). By focusing on papers published post-1953, we selected studies that conceptually linked carrying capacity and ecosystem level phenomena. We compiled a list of 1170 papers by searching for "carrying capacity" and "ecosystem." We used the filter "ecosystem" to limit our review to papers that discussed ecosystem level implications of carrying capacity, irrespective of the scale of the particular study. We refined our search by focusing on articles published within the "environmental science" and "agricultural and biological sciences" subject areas and we excluded studies in the "earth and planetary science" subject area. By doing so, we excluded a number of studies (161) related to the global human population in an entirely different carrying capacity paradigm originally developed by Vogt (Vogt (1948); (Fig. 1a)).

We examined the abstracts of the resulting 822 papers to limit our investigation to studies that explicitly tested carrying capacity concepts using defined metrics. We looked for studies that explicitly: 1) defined carrying capacity; and 2) quantified the carrying capacity in that particular study. We compiled and organized the studies that met these criteria (114 papers) into three different tables by: 1) listing studies by how carrying capacity was defined (Table 1); 2) listing studies by factors or mechanisms that govern carrying capacity (Table 2); and 3) listing studies that discuss the implications and the ecosystem level response of exceeding carrying capacity (Table 3).

3. Results

Among the 114 papers that we reviewed, we found 5 major subject areas where carrying capacity is most often used and applied: aquaculture, rangeland management, wildlife management, conservation biology, and fisheries biology (Fig. 1b). We found that aquaculture studies accounted for 25% (29 papers) of the papers applying carrying capacity; combined, rangeland management and wildlife management accounted for 42% (48 papers), fisheries biology/management accounted for 48% (55 papers), and studies in conservation biology accounted for 55% (63 papers). Summed, the subject areas exceeded the number of papers we reviewed, as some papers spanned multiple subject areas. Of the 63 studies we reviewed in conservation biology, 19 focused on at risk species including: the woodland warbler (Duarte et al., 2016), the numbat (Hayward et al., 2015), and the African lion (Everatt et al., 2014; Kissui and Packer, 2004).

3.1. What exactly are we testing?

Across the disparate and wide-ranging ecosystem studies that use the carrying capacity framework, we found over 19 explicit permutations of carrying capacity with overlapping levels of similarity among the variations. Not surprisingly, most of the applications quantified the number of individuals in an area, with or without explicitly acknowledging K as the historical variable representing carrying capacity (Table 1; e.g. (Melero et al., 2014; Pool et al., 2014; Treydte et al., 2001)). Besides studies that tested the number of individuals in a particular area with carrying capacity, we found studies that quantified: 1) the oxygen carrying capacity of hemoglobin (Dabruzzi and Bennett, 2014; De Domenico et al., 2013; Tufts et al., 2013); 2) the

Table 1
Explicit definitions of carrying capacity in ecosystem studies.

Definition of carrying capacity	Study
Surface area	Pagel et al. (2014)
Swan days (Swans*days)	Wood et al. (2014)
Regression model relating lion density to biomass of preferred prey species	Everatt et al. (2014)
Number of individuals in an area	Pool et al (2014), Aryal et al. (2014), Campos and Jack (2013), Gray et al. (2012), Nilsson et al. (2011), Okayasu et al. (2011), Gliwicz et al. (2010), Cheyne (2006), Gaston et al. (2003), Zambrano et al. (2001), Bjorndal et al. (2000), Comeau et al. (2015), Golluscio et al. (2015), Hayward et al. (2015), Huntsman and Petty (2014), Moore (2013), Weckel and Rockwell (2013), Siamudaala et al. (2012), Peeters et al. (2010), Perry and Bond (2009), Nedorezov et al. (2008), Perry and Schweigert (2008), Crawford et al. (2007), Moran and Bjorndal (2005), López-Sepulcre and Kokko (2005), Kissui and Packer (2004), Ruiz-Olmo et al. (2001), Nagpal et al. (2000), Madenjian et al. (1998), Larsen and Hesthagen (1995)
Number of individuals in an area, K	Melero et al. (2014), Fukasawa et al. (2013), Watari et al. (2013), Huang et al. (2012), Stewart et al. (2009), Bradshaw et al. (2006), Hendriks et al. (2005), Pujoni et al. (2016), Duarte et al. (2016), MacCracken et al. (2014), Braithwaite et al. (2012), Donovan et al. (2012), Zehnder and Hunter (2008), Hansen et al. (2007), Flatt and Scheuring (2004), Byappanahalli et al. (2003), Nakamaru et al. (2002), Treydte et al. (2001), Preston and Snell (2001), Kilmer and Probert (1977, 1979)
Rainfall and past temperature to infer large herbivore CC	Rodríguez et al. (2014)
Highest "sustainable" animal units per area/ production potential	Strassburg et al. (2014), Silva et al. (2011), Xu et al. (2011), Guyondet et al. (2010), Filgueira et al. (2014a, 2014b, 2014c), Ibarra et al. (2014), Byron et al. (2011), Ratan and Singh (2013), Filgueira et al. (2010), Guyondet et al. (2014), Filgueira and Grant (2009), Grant et al. (1995), Das and Shivakoti (2006), Njoka and Kinyua (2006), Jiang and Gibbs (2005), Ferreira et al. (1997), Smaal et al. (1997)
Spatial gradient of energy availability for individuals in an area	Hurlbert and Stegen (2014)
Biomass per area	Feuereisel and Ernst (2009), García-Rubies et al. (2013), Heyman (1983), Kutlu et al. (2014), Lin et al. (2013), Maury et al. (2007), Thébault et al. (2008), Wabnitz et al. (2010)
Syntaxonomic diversity	Redžić (2007)
Size	Mayer et al. (2006)
Mass of carbon per area	Keith et al. (2010), Li et al. (2015)
Oxygen carrying capacity of hemoglobin	Dabruzzi and Bennett (2014), De Domenico et al. (2013), Tufts et al. (2013)
Carrying capacity of greenhouse gas emissions	Worrall and Clay (2012)
Particulate organic carbon CC	Sanz-Lázaro et al. (2011)
Soil water CC for vegetation	Wang et al. (2008)
Foraging behavior	Morris and Mukherjee (2007)
Organic CC for aluminum	Cory et al. (2006)
Primary production for fishery	Vasconcellos and Gasalla (2001)

Table 2
Factors governing carrying capacity in ecosystem studies. Though there is some thematic overlap in categories, we found over a dozen different mechanisms governing carrying capacity in ecosystems.

Factors Governing Carrying Capacity	Study
Climate	Heyman (1983), Guyondet et al. (2014), Scheidt and Hurlbert (2014)
Metabolizable energy	Feuereisel and Ernst (2009), Filgueira et al. (2014a, 2014b, 2014c), Ismail and Jiwan (2015)
Energy Content/availability	Jiang and Gibbs (2005), Perry and Schweigert (2008), Thébault et al. (2008), Guyondet et al. (2010, 2014), Peeters et al. (2010), Wabnitz et al. (2010), Byron et al. (2011), Hurlbert and Stegen (2014), Wood et al. (2014)
Top down anthropogenic pressure	García-Rubies et al. (2013), Everatt et al. (2014)
Habitat availability	Gaston et al. (2003), López-Sepulcre and Kokko (2005), Cheyne (2006), Perry and Bond (2009), Huang et al. (2012), Donovan et al. (2012), Siamudaala et al. (2012), Braithwaite et al. (2012), Moore (2013), Campos and Jack (2013), Watari et al. (2013), Fukasawa et al. (2013), Pool et al. (2014), Huntsman and Petty (2014), Strassburg et al. (2014), Duarte et al. (2016)
Food availability	Ferreira et al. (1997), Bjorndal et al. (2000), Nagpal et al. (2000), Byappanahalli et al. (2003), Moran and Bjorndal (2005), Das and Shivakoti (2006), Grant et al. (1995), Morris and Mukherjee (2007), Crawford et al. (2007), Zehnder and Hunter (2008), Filgueira and Grant (2009), Gliwicz et al. (2010), Xu et al. (2011), Jia et al. (2012), Ratan and Singh (2013), Watari et al. (2013), Melero et al. (2014), Huntsman and Petty (2014), Filgueira et al. (2014a, 2014b, 2014c), Hayward et al. (2015)
Prey availability	Ruiz-Olmo et al. (2001), Zambrano et al. (2001), Aryal et al. (2014)
Primary productivity	Smaal et al. (1997), Vasconcellos and Gasalla (2001), Bradshaw et al. (2006), Maury et al. (2007), Keith et al. (2010), Worrall and Clay (2012), Rodríguez et al. (2014), Guyondet et al. (2014), Li et al. (2015), Golluscio et al. (2015)
Exposure to toxic substances	Preston and Snell (2001), Nakamaru et al. (2002), Hendriks et al. (2005)
Omnivory/ Herbivory	Golluscio et al. (2015), Pujoni et al. (2016)
Mortality	Ibarra et al. (2014)
Hydrodynamics, water temperature and flow	Larsen and Hesthagen (1995), Filgueira et al. (2014b)
Nutrients	Heyman (1983), Kutlu et al. (2014)
Disease	Kissui and Packer (2004)
Frequency of sex	Flatt and Scheuring (2004)

Table 3
The ecosystem responses of exceeding carrying capacity varied throughout the literature. Most of the implications found in the literature were related to a decrease in ecosystem productivity.

Ecosystem Response	Study
Decrease in biodiversity	Gaston et al. (2003), Thébault et al. (2008), Stewart et al. (2009), Gliwicz et al. (2010), Sanz-Lázaro et al. (2011), Huang et al. (2012), Watari et al. (2013), Pool et al. (2014), Socolar et al. (2015)
Decrease in productivity	Bjorndal et al. (2000), Moran and Bjorndal (2005), Grant et al. (1995), Perry and Schweigert (2008), Wang et al. (2008), Filgueira and Grant (2009), Filgueira et al. (2010, 2014a, 2014b, 2014c), Byron et al. (2011), Ratan and Singh (2013), Weckel and Rockwell (2013), Rodríguez et al. (2014), Wood et al. (2014), MacCracken et al. (2014), Ismail and Jiwan (2015), Comeau et al. (2015), Golluscio et al. (2015)
Decrease in C sequestration (including increases in soil C loss)	Zehnder and Hunter (2008), Keith et al. (2010), Worrall and Clay (2012), Strassburg et al. (2014), Groffman et al. (2015)
Changes in biogeochemical cycling (e.g. C, N, P cycle dynamics)	Nagpal et al. (2000), Zehnder and Hunter (2008), Guyondet et al. (2010, 2014), Filgueira et al. (2010), Kutlu et al. (2014)
Increase in non-native invasions	Watari et al. (2013), Fukasawa et al. (2013), Melero et al. (2014), Comeau et al. (2015)
Ecosystem state change, trophic cascade/ interactions, ecosystem collapse, ecosystem destability	Kilmer and Probert (1979), Vasconcellos and Gasalla (2001), Zambrano et al. (2001), Jiang and Gibbs (2005), Mayer et al. (2006), Filgueira et al. (2014a)

"sustainable" production carrying capacity of several commercially important animals, where "sustainable" is defined based on context specific parameters, such as level of phytoplankton depletion (Filgueira et al., 2010, 2014a; Guyondet et al., 2014; Strassburg et al., 2014; Xu et al., 2011); 3) the carrying capacity of game, given a particular biomass of plants in a given area (Feuereisel and Ernst, 2009; Wabnitz et al., 2010), though when carrying capacity was first applied to biological systems, the concept was applied to mostly mobile animals and not plants; and 4) the carrying capacity biomass for animals in a given area (García-Rubies et al., 2013; Lin et al., 2013). We also found several categories of lesser-used carrying capacity studies based on: 1) surface area (Pagel et al., 2014); 2) syntaxonomic diversity (Redžić, 2007); 3) soil water carrying capacity to support plant primary productivity (Wang et al., 2008); 4) the carrying capacity of carbon in a particular ecosystem (Keith et al., 2010; Li et al., 2015); and 5) energy carrying capacity (Hurlbert and Stegen, 2014).

3.2. Molecules to landscapes

Carrying capacity is applied across all scales of ecological organization (Monte-Luna et al., 2004). Out of the 114 papers that we analyzed, 2% used carrying capacity at the cellular/molecule level (3 papers), 59% at the population level (67 papers), 2% at the community level (3 papers), 35% at the ecosystem level (40 papers), and less than 1% at the landscape level (1 paper). As an example—and perhaps most true to its historical application—as previously mentioned above, carrying capacity has been applied at the molecular level to describe the oxygen carrying capacity of hemoglobin and how that relates to animal anatomy and physiology (Dabruzzi and Bennett, 2014; Tufts et al., 2013).

4. Discussion

The high number of studies in rangeland and wildlife management suggests that the contemporary usage of the carrying capacity concept is informed by its historical evolution. For example, as we discussed above, one of the first applications of carrying capacity in the figurative sense was to discuss rangeland productivity and cattle grazing on grasslands (Thomson, 1887). In their review of range science, Sayre and Fernandez-Gimenez (2003) highlighted the evolution of carrying capacity and its adoption in rangeland management ultimately from the engineering "payload" context. Our results suggest that the historical use of carrying capacity has continued to inform its importance to the rangeland and wildlife management fields today.

Concepts such as population size, "carrying capacity," and population dynamics have long been central in the fields of wildlife management and conservation biology (Shaffer, 1981). Because conservation biology is often concerned with single species at risk for extinction and focus on the population level, it is intuitive that these studies use carrying capacity to investigate species viability. Given that conservation biologists and wildlife managers are historically most often interested in populations and dynamics of populations, including concepts such as birth rates, death rates, and K—the intrinsic limit of a population—the application of carrying capacity in wildlife management and conservation biology is a natural extension and application of the concept.

Though we found that the majority of the contemporary usage of carrying capacity was in subject areas that have a legacy of application, ecosystem studies in aquaculture have recently adopted carrying capacity. For example, the earliest applications of an explicitly defined approach using carrying capacity in aquacultural ecosystems we found in this study—there are earlier examples of carrying capacity used in aquaculture studies (see Carver and Mallet, 1990; Incze et al., 1981)—was in 1997 when four papers appeared in the same issue of *Aquatic Ecology* (Dame and Prins, 1997; Dowd, 1997; Ferreira et al., 1997; Smaal et al., 1997). These studies focused on quantifying potential bivalve biomass for culture and discussed bivalve carrying capacity in terms of "water mass residence time, primary production time, and bivalve clearance time" (Dame and Prins, 1997). In contrast to conservation biology and rangeland and wildlife management, the use of carrying capacity in ecosystem studies within aquaculture is a more recent phenomenon. Though the carrying capacity concept has clear theoretical origins and is attributed to the logistic function of Verhulst (1838) and the Odum (1953) assertion that the asymptote of the logistic curve is a “carrying capacity,” the contemporary definition of carrying capacity is wide-ranging and its application extends beyond the number of individuals in a given space.

4.1. Carrying capacity across scales of biological organization

Carrying capacity is most often used at the population level to describe an ecosystem's ability to “support” a specific and often fixed number of species. At this level, we found a range of studies that: 1) modeled a range of moths that a plant could support (Nedorezov et al., 2008); 2) quantified the carrying capacity of perennial grass (Fowler and Pease, 2010); 3) quantified the impacts of climate change on the white throated dipper (Nilsson et al., 2011); and 4) modeled the impacts of fishing on marine mammals in the management context (Moore, 2013).

Though energy flow is not often explicitly considered in population level studies, Akbaripasand et al. (2014) explicitly investigated the metabolic demand required of a single species of fish. They quantified the energy budget of a species of fish in a stream ecosystem. Given that population dynamics are often modeled with the equation attributed to Verhulst (1838), the relatively high number of population level studies that use the carrying capacity concept was not surprising.

At higher levels of ecological organization—community, ecosystem, and landscape—the carrying capacity concept is often modified to explicitly incorporate principles of community competition, ecosystem energy flows or material cycling, and landscape patches and pattern, depending on the scale of study. For example, in one of the few community level studies using carrying capacity, Pagel et al. (2014) quantified waterfowl metacommunity recovery using a “nested subsets” theory following ecosystem protection, a theory that measures ecosystem structure by analyzing either species-site interaction or species-species interactions. In another study, Hurlbert and Stegen (2014) used community metrics, such as species richness and phylogenetic structure to analyze the relationship between ecosystem energy availability and species richness. In the final community level study we found in our search, Leary and Petchey (2009) tested the “insurance hypothesis”—the idea that increasing species richness has a stabilizing effect on communities and ecosystems—in laboratory microcosms.

At the ecosystem level, we found studies that used carrying capacity to investigate fundamental principles in ecosystems such as energy flow and material cycling. This includes studies that: 1) used a Dynamic Energy Budget (DEB) ecosystem model to investigate the impacts of shellfish on the marine food web (Filgueira et al., 2014b; Guyondet et al., 2010; Peeters et al., 2010); 2) quantified the magnitude of grazing at which the flux of greenhouse gas was equal to the sink of peat soils (Worrall and Clay, 2012); and 3) used various permutations of quantifying the mass of carbon that a particular ecosystem can sequester (Keith et al., 2010; Li et al., 2015) or in the case of fish farming, the load and impact of organic carbon deposition on the benthos (Sanz-Lázaro et al., 2011). At the ecosystem level in the Patagonian steppe, rangeland carrying capacity has been defined as a function of aboveground net primary production (ANPP), a “sustainable harvest” index, and as the fraction of ANPP consumed (Golluscio et al., 2015). When carrying capacity is applied to ecosystem level studies, it is modified to test principles of ecosystem ecology, such as the movement of energy and matter through the system.

We found only 1 study in our review that applied carrying capacity at the landscape level. Donovan et al. (2012) used a concept borrowed from graph theory and habitat suitability maps to quantify the number of individuals in an area that any given landscape may support. For example, Donovan et al. (2012) calculated the number of ovenbirds and bobcats that could coexist in a given northeastern landscape area based on a maximum clique analysis, a computationally intensive analysis based on habitat suitability maps for each species. Carrying capacity is rarely applied to landscape level studies, and we speculate that this may be attributed to the difficulty of incorporating landscape principles in a carrying capacity context or modifying carrying capacity concept for landscape analyses.

Despite the theoretical origin of carrying capacity and its use to model species interactions and population dynamics at the population level, our results suggest that carrying capacity is widely used across all levels of ecological organization (see also Monte-Luna et al., 2004). Our results also suggest that carrying capacity is modified to incorporate principles of each level of ecological organization for which it is applied: 1) at the molecular level, atoms are the subjects “carrying”; 2) at the population level, numbers of species and the interaction of species is of interest; 3) at the ecosystem level, the carrying capacity incorporates energy and materials; and 4) at the landscape level, patches and patterns are incorporated.

4.2. Carrying capacity over time and space

While the logistic equation from Verhulst (Verhulst (1838); Equation (1)) may be used to model changes in population sizes over time, it is unclear whether carrying capacity should be understood as a fixed entity as it was originally applied (Fig. 1a), or as variable as it has been commonly applied since Odum (1953) named the asymptote of the logistic curve as “carrying capacity” (Sayre, 2008). In our review, we found considerable differences among the reviewed studies with how time and space are considered. For example, we found studies that implicitly and/or explicitly explored the variation of a carrying capacity over time and space (Duarte et al., 2016; Groffman et al., 2015; Pujoni et al., 2016). We also found studies that did not implicitly or explicitly consider variation of carrying capacity over time and space (Golluscio et al., 2015; Ismail and Jiwan, 2015). In studies that considered carrying capacity dynamic with respect to time, scenarios or simulations were most frequently used to quantify the variation in populations and in carrying capacity (Filgueira et al., 2014b; Ibarra et al., 2014; Melero et al., 2014). For example, in their study to model production potential of shellfish through aquaculture, Ibarra et al. (2014) implemented several one year simulations of mussel population dynamics by varying the initial mussel stocking density. Ibarra et al. (2014) defined production carrying capacity as "the smallest initial mussel density that produced the highest harvest yield." At the end of their one-year simulations, they found highest production carrying capacities at intermediate stocking densities because food limitation led to a decrease in production carrying capacity at high initial stocking densities. Given the goals of mussel producers, the emphasis on production carrying capacity is largely an economic rationale.

To account for temporal and spatial population variability in their study of production potential in oysters, Filgueira et al. (2014b) used a spatially explicit ecosystem model to simulate the effects of bivalve grazing on phytoplankton. Stocking filter feeders, such as bivalves, at high density negatively impacts the phytoplankton in the system and often limits shellfish production (Grant et al., 1995; Ulanowicz and Tuttle, 1992). Filgueira et al. (2014b) used 5 scenarios to quantify the impacts of increasing the standing stock biomass of oysters on phytoplankton and determined the carrying capacity of oysters based on a depletion index of phytoplankton. Using the bay scale index of phytoplankton depletion, Filgueira et al. (2014b) demonstrated how spatial variability within an ecosystem influences the production carrying capacity of shellfish. Given that the number of individuals that an ecosystem can support—a concept in population biology with ties to carrying capacity—is strongly linked with ecosystem productivity and that ecosystem productivity is spatially variable, it is not surprising that many of the studies that we reviewed explicitly considered the spatial dependence of carrying capacity.

4.3. Mechanisms governing CC

Despite the ambiguity, wide-ranging, and multidisciplinary application of carrying capacity, our review of the literature revealed several common mechanisms that govern carrying capacity, either explicitly or implicitly. That is, a large proportion of the studies we reviewed—83 out of the 114 studies—discussed controls that governed carrying capacity in the context of that specific study (Table 2). Fundamentally and perhaps unsurprisingly, we found that carrying capacity was controlled by resource availability. However, several more specific mechanisms govern carrying capacity and highlight the extent that carrying capacity is modified in a context-specific manner. For example, we found that food, space, and available energy were the most common regulators of carrying capacity, accounting for nearly half—41 out of 83—of the studies that identified a carrying capacity control, although more than a dozen mechanisms have been proposed to govern carrying capacity in ecosystems.

In general, studies that used carrying capacity in an animal production perspective (i.e. to maximize biomass for consumption)—the rangeland management and aquaculture fields—were more likely to discuss food as a limitation of ecosystem production and a control of ecosystem carrying capacity.

Another emergent and prevalent control over ecosystem carrying capacity was habitat or space availability. Space has been reported to be a regulator of carrying capacity for moths (Nedorezov et al., 2008), fish populations in marine systems and freshwater streams (Perry and Bond, 2009; Perry and Schweigert, 2008), and ungulate population size over geological scales (Rodríguez et al., 2014). The importance of space or habitat for regulating carrying capacity was prevalent in the conservation biology literature. For example, space availability is an important mechanism governing carrying capacity for: snow leopard biomass in conservation areas (Aryal et al., 2014); the biomass of Ecuadorian Capuchin in fragmented forests (Campos and Jack, 2013); and understanding reintroduced numbat population dynamics in Australia (Hayward et al., 2015). To combat the risks of species extinctions, conservation biologists often propose conserving high-value habitat (Noss et al., 1997). For this reason, it is not surprising that studies in conservation science often specify habitat or space as a factor governing carry capacity. In other words, habitat and space are often used as currencies for endangered species conservation. To interpret this more literally, space in conservation science is akin to biomass production in bivalves or money for a business. Although the carrying capacity approach houses a spectrum of diverse studies and research fields, carrying capacity is fundamentally governed by resource availability and specific governing factors depend on study and context.

4.4. Implications of CC overshoot

Among the ecosystem studies that we reviewed, many implications of "overshooting" the ecosystem carrying capacity were discussed. While our analysis did not consider the effects of the duration of carrying capacity overshoot, we provide a conceptual overview of the ecosystem level effects of carrying capacity overshoot (Fig. 2) and a list of studies that address implications of exceeding ecosystem carrying capacity (Table 3). The most common ecosystem-level implications of overshooting carrying capacity in the studies that we reviewed were: 1) a decrease in species biodiversity and richness (Sanz-Lázaro et al., 2011; Socolar et al., 2015; Thébault et al., 2008); 2) a decrease in primary productivity (Byron et al., 2011; Perry and Schweigert, 2008; Ratan and Singh, 2013); 3) changes in biogeochemical cycling (Filgueira et al., 2010; Groffman et al., 2015; Guyondet et al., 2010, 2010); and 4) an increase in the vulnerability to invasions (Comeau et al., 2015; Fukasawa et al., 2013; Melero et al., 2014). In addition to these 4 commonly discussed implications of overshooting carrying capacity, several studies discussed decreases in carbon sequestration (Groffman et al., 2015; Strassburg et al., 2014; Zehnder and Hunter, 2008).

Several studies have suggested that overshooting carrying capacity may lead to larger magnitude ecosystem impacts. For example, we found studies that discussed large scale ecosystem change, such as ecosystem state/regime change/thresholds in

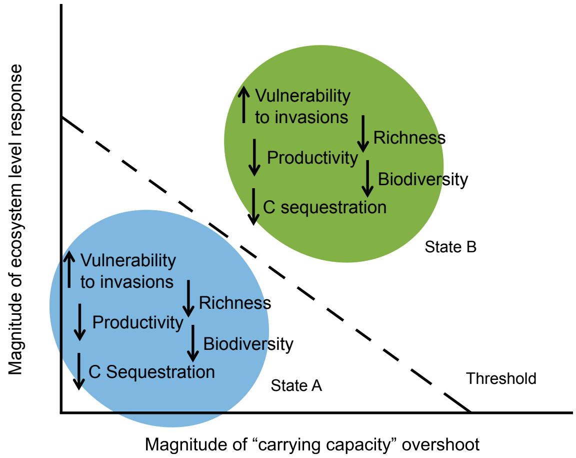

Fig. 2. Implications of "overshooting" the carrying capacity in reviewed ecosystem studies. Most reviewed studies report a decrease in ecosystem productivity and biodiversity as implications of overshooting carrying capacity. If the magnitude of overshoot is great enough, the ecosystem passes a threshold (dotted line) and changes ecosystem state (different color of oval), where continued carrying capacity overshoot further elicits an ecosystem response.

the context of carrying capacity (Mayer et al., 2006), trophic cascades/ecosystem collapse (Zambrano et al., 2001), and ecosystem destability (Kilmer and Probert, 1979).

As a whole, the evaluated studies suggest that the magnitude of the ecosystem level response depends on the magnitude of carrying capacity overshoot (Fig. 2). For example, at a relatively small magnitude of carrying capacity overshoot, a small magnitude ecosystem response—a small decrease in primary productivity or a small decrease in biodiversity—would be expected. However, if the magnitude of carrying capacity overshoot is large enough, a threshold may be crossed and the ecosystem may change states (Fig. 2). Once in the alternate state, a small magnitude carrying capacity overshoot in the new state may lead to new additional changes in biodiversity, ecosystem productivity, or elemental cycling, whereas a large magnitude carrying capacity overshoot may lead to more impactful changes related to ecosystem stability or state changes (Kilmer and Probert, 1977). Our review of the literature—particularly with regards to the implication of carrying capacity overshoot—highlights the broad application of carrying capacity across research disciplines. The concept often envelopes disparate and discipline-specific themes under one research area, whether it be population dynamics, biogeochemistry, or landscape pattern.

5. Conclusions

Given its convoluted history, theoretical elegance, multidisciplinary application, and the variation of application within each field, it is not surprising that carrying capacity is both widely used and criticized. Carrying capacity is a widely familiar concept; serial historical applications have given the approach an authoritative influence across disciplines. The concept is often indiscriminately adopted with little knowledge of why it is used in the discipline. As a result, carrying capacity incorporates disparate and fundamental concepts in biology across all levels of ecological organization including, diffusion at the atomic and cellular level, competition and population dynamics at the population level, available energy and materials at the ecosystem level, and patches, pattern, and configuration at the landscape level. Nevertheless, there are underlying themes and similarities with studies that apply carrying capacity.

Though there are several themes and common approaches used in carrying capacity studies that we highlighted in our study, we argue that uncritical adoption of carrying capacity leads to nonunified applications of the framework. Because the use and application of carrying capacity is wide-ranging and context specific, we argue that the unifying value of the concept is lost.

Our review of the application of carrying capacity in ecosystem studies showed that: 1) because of its strong historical ties to population dynamics, carrying capacity is most often applied at the population level—commonly defined as the number of individuals per unit area—though there were over a dozen explicit definitions across all levels of ecological organization; 2) carrying capacity is often considered dynamic with relation to both time and space; 3) carrying capacity is distally controlled by energy availability and proximally by habitat and food availability; 4) when required resources exceed available resources there are negative impacts on ecosystems including, a decrease in productivity, biodiversity, and richness, and an increase in vulnerability to invasion; and 5) there are several links among carrying capacity, ecosystem states, and ecosystem stability.

We end with several suggestions for the application of the carrying capacity concept for future carrying capacity studies. We argue that future carrying capacity studies should: 1) explicitly state assumptions of a static or variable carrying capacity; 2) use "unpackaged" and deliberate language to explicitly state the particular ecological concepts of the study; 3) frame the study with fundamental and quantitative ecological principles across all levels of biological organization; and 4) be modified for the particular application. For example, in shellfish aquaculture studies, fundamentally, the “production carrying capacity” represents the maximum “sustainable” biomass of shellfish that can be produced without having negative impacts on phytoplankton and other parts of the food web (e.g. Filgueira et al., 2010; Ibarra et al., 2014) and strongly depends on ecosystem primary productivity. In this example, framing ecological production of shellfish in terms of universal ecological concepts such as primary productivity circumvents the linguistic issues of “carrying capacity” while providing a quantitative assessment of an ecosystem's ability to provide ecosystem services. Furthermore, this particular example highlights the extent to which carrying capacity is linked to social concepts such as “acceptability” and how “negative impacts” are defined. By incorporating these suggestions, future ecosystem carrying capacity applications may avoid some of the historical critiques of the carrying capacity concept.

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