

Density dependence: an ecological Tower of Babel

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Abstract The concept of *density dependence* represents the effect of changing population size on demographic rates and captures the demographic role of social and trophic mechanisms (e.g. competition, cooperation, parasitism or predation). Ecologists have coined more than 60 terms to denote different statistical and semantic properties of this concept, resulting in a formidable lexicon of synonyms and polysemies. We have examined the vocabulary of density dependence used in the modern ecological literature from the foundational lexicon developed by Smith, Allee, Haldane, Neave and Varley. A few simple rules suffice to abate terminological inconsistency and to enhance the biological meaning of this important concept. Correct citation of original references by ecologists and research journals could ameliorate terminological standards in our discipline and avoid linguistic confusion of mathematically and theoretically complex patterns.

Keywords Allee effect · Demographic rate · Density feedback · Population dynamics · Regulation · Terminology

Biologists do not apply the term ‘chromosome’ to any coloured body
(Varley 1958)

Introduction

Most ecologists would agree with a definition of density dependence as “...a dependence of per capita population growth rate on present and/or past population densities” (Murdoch and Walde 1989). Behind such a *simple* definition lies a long history of debates that has ramified into a colourful body of jargon. Inconsistencies in the lexicon used to denote statistical and semantic properties of density dependence, and associated population phenomena and mechanisms (Berryman et al. 2002; Cooper 2001; Murray 1982; Sale and Tolimieri 2000), have nourished an old debate through ecology’s infancy (Andrewartha 1958, 1959; Nicholson 1958, 1959; Varley 1959), maturation (den Boer 1968; Hanski et al. 1993; Krebs 1995; Reddingius 1971; Slobodkin et al. 1967; Strong 1986; Wolda 1995) and modern sophistication (Berryman 2004; Bjørnstad and Grenfell 2001; Krebs 2002a; Murray 2001; White 2008). This debate has contrasted (in simple terms) the demographic roles of biotic interactions (as inferred from density dependence) and stochastic and abiotic factors, and has focussed on how to provide quantitative evidence for those roles in the single-most important theme

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of ecology: what determines population numbers? (Elton 1927; May 1999).

The heated and recurring bouts of scientific confrontation have been themselves one of the main reasons for diversification of the lexicon by authors massaging an array of terms to ground their views. As early as the 1950s, entomologists were striving to tidy up the large jargon concerning *density dependence* (hereafter referred to as ‘DD’) (Solomon 1949, 1958; Milne and Solomon 1958; Varley 1958; Milne 1962). Since then, this lexicon has kept expanding into an imposing collection of synonymies and polysemies, driving a pervasive inconsistency in the literature and potentially threatening communication across authors, publications and disciplines. Far from dissuading authors from using density dependence, the polemics have emboldened this concept, likely boosting its currently wide cross-taxa and -discipline usage—at the expense of terminological standards and ecological clarity.

Through this first historical examination of the DD terminology, we herein track the genesis of this term (*density dependence*) and its related lexicon (*Allee effect*, *density feedback*, *self-thinning*) and currently used qualifiers (*compensatory*, *direct*, *delayed*, *depensatory*, *inverse*, *negative*, *positive*). We show that simple rules of nomenclature suffice to abate pervading terminological inconsistency and to enhance the biological meaning of the concept. We expect this study to become a reference tool for early-career researchers as they become confronted with the voluminous literature on density dependence, as well as for scholars and experts who might consider making a conscious selection of terms with respect to the foundational studies. Our overarching aim is to emphasize that a more precise terminology is required for any discipline with solid and unified foundations, which can facilitate communication between ecologists in different fields of research and degrees of expertise and, ultimately, contribute to drawing generalities around the complex dynamics of populations across taxa, ecosystems, methods and disciplines. We complement our argument with three appendices [Electronic Supplementary Material (ESM)], comprising a sketch of a demographic feedback and examples of studies accounting for DD (ESM Appendix 1), extended reasoning for inflation of the DD jargon (ESM Appendix 2) and an illustration of usage of our proposed lexicon (ESM Appendix 3).

The concept—not the term

Historically, the concept substantiating DD is distilled from Malthus’ thinking on limits to growth in human demography (Malthus 1798), Darwin’s views on natural selection and the struggle for existence (Darwin 1859), the popularization of the

logistic curve (Kingsland 1995; Pearl 1925; Verhulst 1838), some of the earliest and most influential treatises of ecology (Elton 1927; Fisher 1930) and from among the precursors of general systems theory in which individuals are treated as molecules exchanging matter and energy in a dynamic matrix (Adams 1918).

Harper (1974) attributed the first conceptualization of DD into a mathematical model to the Swiss botanist Karl Wilhelm von Nägeli (1874). Botanists had certainly founded the study of competition and population dynamics through the nineteenth (e.g. DeCandolle, Sachs, Wollny) and early twentieth (e.g. Clements, Sukatschew, Tansley) centuries, addressing DD questions in field observations and experimental manipulations of plant densities (reviewed in Clements et al. 1929): “There are certain points of resemblance between communities of plants and those of human beings or animals; one of these is the competition for food which takes place between similar individuals and causes the weaker to be more or less suppressed” (Warming 1909). Over the first third of the twentieth century, zoologists embraced DD in the study of animal demography within two main fields, namely the biological control of insect pests (Howard and Fiske 1911; Smith 1935; Thompson 1928) and the physiology and demography of protozoans in laboratory cultures (Johnson 1933; Robertson 1924; Woodruff 1911). Entomologists emphasized the prevention of population growth rates by crowding due to increased predation/parasitism on outbreaking insects, while protozoologists did so with increased mortality resulting from accumulation of toxins of thriving protozoa. Warder Allee married the advances of the two disciplines in the promotion of DD and amplified its semantics with those cases where population growth rates were measured in groups of living beings benefitting from some degree of *aggregation* (Allee 1927) or *cooperation* (Allee 1931b). Allee borrowed the principles of cooperation from the earliest scientists who studied animal societies systematically (e.g. Éspinas, Kropotkin and Wheeler whom Allee cited frequently) and adopted terminology from fellow botanists (Clements and Shelford 1939) to apply it to animal demography (Allee 1927, 1931a, b). Due to his pioneering broad view of DD, we believe that Allee could claim fatherhood of this concept in ecology.

Mathematically, DD is a statistical signal of a (causal) relationship between the size of a population and at least one of its measurable demographic rates. Thus, the demographic rate represents the response variable, and population size functions as the predictor. DD can be measured by three statistical properties: (1) evidence [relative statistical support for the DD relationship through estimates of Type I error probability (Fox and Ridsdill-smith 1995), model probabilities (Brook and Bradshaw

2006) or parameter goodness-of-fit (Dennis et al. 2006)]; (2) strength [slope of a linear relationship (May 1974; May et al. 1974)]; (3) shape [degree of nonlinearity (Fowler 1981; Gilpin and Ayala 1973)]. Strength measures changes in a demographic rate in response to unit (raw scale) or order-of-magnitude (proportional scale; e.g. logarithmic) changes in population size. As to shape, upwardly curved DD growth responses imply that most DD (i.e. the highest rate of change in a demographic rate) happens at a relatively high population size, and downwardly curved DD growth responses imply that most DD takes place at a low population size.

In most demographic studies, population size is estimated as the number of individuals per unit area or volume (density), but DD applies equally to absolute numbers or biomass where the entire or a consistent fraction of the population is surveyed. Alternatively, demographic rates encompass fertility, survival, dispersal or their compound interplay in an overall population rate of change generically known as ‘population growth rate’—i.e. change in population size between two consecutive time steps due to losses (mortality, emigration) and gains (fertility, immigration) of individuals (Herrando-Pérez et al. 2012; Sibly and Hone 2002). The effects of population size on growth rates are popularly gauged through population growth curves, such as logistic equations, in which the calculation of sustainable yields has a fundamental application in conservation and management (Eberhardt et al. 2008; Henle et al. 2004; Sabo et al. 2004).

In the ecological context, DD studies ultimately investigate the demographic role of social and trophic interactions (cannibalism, competition, cooperation, disease, herbivory, mutualism, parasitism, parasitoidism, predation, reproductive behaviour and the like) between individuals within a population (Courchamp et al. 1999; Sinclair 1989; Stephens and Sutherland 1999; Turchin 1995) because the intensity of these mechanisms varies with population size. Social and trophic interactions affect demographic rates; in turn, the change in demographic rates alters population size, looping back to modify the intensity of social and trophic interactions (ESM Appendix 1). Such loops constitute a ‘density feedback’ (Berryman 1989; Berryman et al. 2002). In tests, models, experiments and surveys accounting for this feedback (ESM Appendix 1), ecologists use the statistical relationship between population size and a demographic rate as a signal for the ecological relationship between social or trophic interactions and that demographic rate, hypothesizing that the latter will follow the former. In reality, population size is used as a statistical surrogate for how organisms interact at different density ranges.

Genesis of the modern vocabulary

From the beginning of the twentieth century, ecologists have coined more than 60 different DD terms, often in relation to population stability or instability (variance of population size) known to be (at least partly) driven by social/trophic interactions in wild populations (Tables 1, 2). Throughout, the DD terminology has mainly adopted the formula ‘qualifier + density-dependent’, together with other peculiar terms, such as *centripetality* (Caughley and Sinclair 1994), *depensatory* (Neave 1953), *disoperation* (Allee et al. 1949) or *self-thinning* (Shinozaki and Kira 1956). A total of 12 of those terms persist across all disciplines in the modern ecological literature from their genesis, mostly by the 1950s. In the following sections, we review the biography of those foundational terms and identify their synonymies and polysemies.

Density-dependent

Botanists initially branded a variety of generic terms, such as *priority*, *dependence*, *mutuality* (Yapp 1925), *tolerance* (Burns 1920), *reaction* or *coaction* (Clements et al. 1929), to categorize sorts of relationships among neighbouring plants and between the latter and their environmental requirements (light, water etc.). Among zoologists, the entomologists Howard and Fiske (1911) featured a *facultative factor* as a biotic one (e.g. disease) that killed more (host) individuals as the population in question increased in abundance (Table 1). Within the same field of insect biocontrol, and after citing his two contemporaneous colleagues, Smith (1935, p. 889) named the former facultative factors *density-dependent mortality factors*, thus giving birth to the adjective *density-dependent* in ecology (Table 1). Smith (1935) further recognized that “...there is still another category which destroys a percentage that decreases as the density increases... this type of mortality factor is of relatively little importance in the determination of average population densities” (i.e. *inverse* DD, see below) without suggesting any particular nomenclature for such a statistical relationship. Harper (1977) noted the synonymy between *density-dependent*, as defined by Smith (1935) for animal populations, and the botanic term *self-thinning* (Shinozaki and Kira 1956) or “...self-adjustment of excess density due to competitive interaction within overcrowded pure stands of higher plants” (Yoda et al. 1963). Noticeably, new DD terms created by zoologists and botanists over the history of this concept have concentrated mainly on temporal or spatial demography, respectively reflecting the distinct life histories of both groups of organisms and different research areas of enquiry (see below).

Table 1 Historical summary of qualifiers used to name density-dependent factors and relationships between demographic rates and population size, and their linkage to temporal phenomena of change in population size (stability, cycles, instability). References are arranged chronologically. Creation of DD jargon peaked in the 1940–1950s, with new terms seeing the light of day in each decade from the 1910 to 2000s

| Stability | Cycles | Instability | Rate related to N | Foundational references |
|---|---|---------------------------|--------------------------------------|---|
| Facultative | | | Mortality/species multiplication | Howard and Fiske (1911) |
| Environmental resistance | | | Reproduction | Chapman (1928) ^b |
| Individualized | | | Mortality | Thompson (1928) |
| | | Co-operation | Survival (in particular) | Allee (1931b) ^c |
| Controlling | | | Offspring production/survival chance | Nicholson (1933) |
| Density-dependent | | | Mortality | Smith (1935) |
| Direct DD | | Inverse DD | Mortality | Allee (1941) |
| Dependent R-factor | | | r | Vouïte (1943) |
| | Delayed DD | | Host/prey mortality | Varley (1947) |
| Disoperation | | | r | Allee et al. (1949) ^c |
| Concurrent | | | (killing) action | Solomon (1949) |
| (Immediate) negative DD | Delayed negative DD | Positive DD | Emigration/mortality/natality/ r | Haldane (1953) |
| Compensatory | | Depensatory | Mortality | Neave (1953) |
| | | Allee's principle | Survival/ r | Odum (1953) |
| | | Underpopulation | r | Andrewartha and Birch (1954) |
| Self-decimation | | Allee type | Oviposition | Fujita (1954) |
| Density governing | | Density disturbing | Mortality | Lysenko (1954) |
| Self-thinning | | | r | Nicholson (1954b) ^d |
| Perfectly/imperfectly DD | | | Mortality | Shinozaki and Kira (1956) ^e |
| Directly density-related | | Inversely density-related | Mortality | Milne and Solomon (1958) |
| Inversely DD | Alternately density-related | Allee growth type | Mortality/reproductive rate/ r | Solomon (1958) |
| Exact compensation/undercompensation | | Overcompensation | r | Odum (1963) |
| | | Positive feedback | Mortality | Varley (1963); Varley and Gradwell (1970) |
| Negative feedback | | Positively DD | r | ca. Slobodkin (1968) |
| Negatively DD | | Allee effect | Per capita birth rate | Reddingius (1971) |
| | Linear or nonlinear first-order process | | r | ca. May (1972) |
| | Linear or nonlinear second-order process/lag effect | | | Royama (1977) |
| Causal/causally/type A DD-Statistical/statistically/type B DD | | | | Royama (1977); Royama (1981) |
| Intensity-dependent | | Parasite load | | Margolis et al. (1982) |
| Effective DD | | Survival/reproduction | | Murray (1982) |

Table 1 continued

| Stability | Cycles | Instability | Rate related to N | Foundational references |
|--|---------------------------------------|------------------------------------|-------------------------|-------------------------------------|
| Explicit DD | | | r | Strong (1986) |
| Centripetality | | Demographic/component Allee effect | r | Caughley and Sinclair (1994) |
| Classical Nicholsonian DD/direct density control | | | Total/component fitness | Stephens et al. (1999) |
| Phenomenological/weak causal/strong causal DD | | | r | Sale and Tolimieri (2000) |
| Compensatory DD | | Depensatory DD | Population size | Cooper (2001) |
| First-order feedback | Higher-order feedback | | r | Rose et al. (2001) |
| Compensatory density feedback | Delayed compensatory density feedback | Depensatory density feedback | r | Berryman et al. (2002) ^f |
| | | Ensemble Allee effect ^d | r | Herrando-Pérez et al. (2012) |
| | | | r | This paper |

N , population size; DD, density dependence/density-dependent; r , overall population growth rate

The hyphenated expression *density-dependent* is the correct one, although the use of *density dependent* is widespread—this is a grammatical issue

^a The terms *ensemble density feedback* and *component density feedback* refer to feedbacks measured on r (total fitness) or single demographic rates (component fitness), respectively (see main text), so both can be depensatory or compensatory; whereas *ensemble Allee effect* is synonymous with *demographic Allee effect* (Stephens et al. 1999), and implies a depensatory density feedback on r at low N

^b Chapman (1928): “The environmental resistance will include the physical factors of the environment. temperature, humidity, etc. and also the biotic factors of the environment, parasites, competitors, etc.”

^c Allee used these terms with an explicit DD meaning, yet *disoperation* can be trailed to Clements (1935) and *cooperation* has use beyond last century. Allee (1941) and many others often used *undercrowding* (=cooperation) and *overcrowding* (=disoperation), which have a diffuse origin in nonhuman-demography literature

^d Nicholson (1954b; see his Fig. 1) classified nine new terms under two different perspectives. On one hand, terms identifying the effects of population size on factors driving population dynamics (factors were named ‘requisites’ under this perspective). On the other hand, terms identifying the effect of driving factors on population size (named ‘density factors’ under this perspective). His ‘reactive responsive requisites’ could be *governing* or *disturbing* which are germane to *direct* and *inverse* DD (Allee 1941), respectively

^e The term *self-thinning* can be tracked back to European and American literature on plant cultivation and gardening from the nineteenth century; however, mid-twentieth century Japanese botanists reinforced its application in demography (see Harper 1977; ESM Appendix 2)

^f Berryman et al. (2002) promulgated the vocabulary from systems theory. Negative feedback operating without lags is known as *first-order process* or *first-order feedback*, while *delayed negative feedback* is germane to *higher-order process* (Royama 1977) or *higher-order feedback* (Berryman et al. 2002)

In all of the foundational terminology from Smith to Neave and Haldane (see below), *density-dependent* prevails as an expression of a statistical relationship between a demographic rate and population size, while the nominalization of this adjective into *density dependence* is contemporaneous (approx. 1970s). Clearly, the usage of the terms *density-dependent* or *density dependence* as such can be prone to vagueness today because it does not scrutinize types of DD. Smith (1935) referred to DD factors as drivers of population stability, invoking the ideas of *balance* or *control*: “Those species which have persisted have done so because their relations with their environment are such that there is an inherent tendency toward stability of numbers”. Along the same rationale, Nicholson (1933, 1954b) constructed a general theory of population dynamics (and a complex library of DD terms; Table 1) where (intra-specific) competition for depletable resources was the main DD factor balancing populations with their environment. This theory has since fuelled much research into population dynamics specifically (reviewed by Hanski 1990; Hixon et al. 2002; Sinclair 1989; Turchin 1995) and ecology as a whole (Kingsland 1996).

Direct, delayed, and inverse density-dependent

Allee’s work on animal aggregations was well-illustrated in his earliest research into freshwater isopods (Allee 1931a). Based on these ideas and others from research on protozoa [e.g. ‘allelocatalytic effect’ in ‘infusoria’ defined as “acceleration of multiplication by the contiguity of a second organism in a restricted volume of nutrient medium” (Robertson 1924)], social insects [e.g. ‘trophalaxis’ as the mutualistic or cooperative bond between parents and offspring (Wheeler 1918)] and animal cells and organisms in general [e.g. ‘prototaxis’ as the tendency to form aggregations (positive prototaxis) or to stay solitary (negative prototaxis), Wallin (1923)], Allee (1941) stated that: “There is another type of density-dependent factor, which recognised by ... entomologists, is dismissed by certain of them as of no importance in population control. I refer to those eliminating influences which take a decreasing percentage of the individuals present as the population increases”. Therein, he proposed the terms *direct density-dependent mortality factors* [synonymous with Smith’s (1935) *density-dependent*] and *inverse density-dependent mortality factors* (Table 1). Such a lexicon depicts change in mortality as being positively (i.e. *directly*) correlated with change in population size, whereas an inverse relationship implies a negative relationship (Table 2). Through inverse DD, Allee (1941) highlighted the benefits of being a group: “...crowding may have a positive survival value for some or all of the individuals. In so far as they operate, the protection furnished by numbers

is shown by the decrease in percentage eliminated by the inverse density-dependent agencies”.

Varley (1947) observed in pest flies that what he called *delayed density-dependent factors* should be used when mortality factors (i.e. predator, parasites, pathogens) operate with time lags (Table 1): “...the parasites and predators also exercise a reciprocal influence on the numbers of the species on which they feed... the percentage of hosts destroyed by the first parasite generation will not increase, but remain unchanged. The number of hosts killed, and therefore the number of parasites emerging in the next generation, will be proportionately greater”. The lag is explained mechanistically by the density check on prey/hosts being retarded until their predators/parasites/pathogens respond functionally (increase in consumption rates) and numerically (increase in numbers) (Sinclair and Pech 1996; Williams and Collins 2008), and typically results in cycles of population size in both prey/hosts and their ‘enemies’. Yet maternal effects, the environment provided by parents to their offspring (Beckerman et al. 2002), as well as life history (Lande et al. 2002) and carry-over effects (Harrison et al. 2011; Ratikainen et al. 2008), have also been proposed to occasion *apparent* delayed DD. Delayed DD is often assessed through autocorrelation coefficients (Moran 1953; Turchin 1990) as well as autoregressive models including, as a predictor, population size lagged over two or more time steps (Royama 1977).

In contemporaneous ecological works, some authors respect Allee’s (1941) nomenclature contrasting *direct* versus *inverse* DD given the sign of the statistical relationship (e.g. Courchamp et al. 2000; Hixon et al. 2002; Jennings 2000; Pech et al. 1992; Sandin and Pacala 2005; Wallin and Raffa 2004). In contrast, others differentiate *direct* and *delayed* DD in terms of whether the density feedback is immediate or retarded (e.g. Bjørnstad et al. 1995; Brook and Bradshaw 2006; Holyoak and Lawton 1992; Saitoh et al. 2006; Williams et al. 2004; Yoccoz et al. 2001). As a result, the term *direct* DD has become pervasively polysemous. Berryman et al. (2002) argued that the reason for such polysemy is that when authors use population growth curves (Eberhardt et al. 2008), the relationship between population size and population growth rate is (1) inverse (negative) for what Allee (1941) called *direct* DD, and (2) direct (positive) for what Allee (1941) called *inverse* DD (Table 2). The former twist of signs and terms simply originate from the fact that Allee used mortality rates instead of population growth rates as a response (Fig. 1)!

Compensatory and depensatory

With reference to salmonids, Neave (1953) propounded the expressions *compensatory mortality factors* as opposed to

depensatory mortality factors (he actually invented the word *depensatory*) to refer to statistical relationships which could be coupled with specific population dynamics: “...mortality which becomes relatively heavier (compensate) as populations *increase* in density, thereby tending to stabilise the prevailing population level”, and “...mortality which becomes relatively heavier (depensate) as populations *decrease* in density, thereby tending to exaggerate fluctuations initiated by other causes” (Neave 1953) (Table 1). Clearly, *compensatory* and *depensatory* are synonymous with *direct* and *inverse* DD, respectively, as used by Allee (1941) (Table 2). The intuitive meaning of compensatory mortality in a demographic context (that is, mortality compensating for increase in population numbers) explains why Nicholson (1954a) already referred to *compensatory reactions* in his classical experiments with blowflies, whereas Varley added another semantic layer to this jargon (see *overcompensation* below).

The terms *compensatory* and *depensatory* DD have been employed predominantly in fisheries papers (e.g. Liermann and Hilborn 1997; Mullon et al. 2005; Myers et al. 1995; Rose et al. 2001; Walters et al. 2008), in which new jargon designed in other disciplines has been largely neglected. Thus, Neave’s (1953) only quotation outside fisheries was: “...for (compensatory) mortality which operates in this manner the term ‘density-dependent mortality’ has been used in other fields, particularly in entomological studies (Solomon 1949)”. Curiously, due to his dual expertise on

stonefly taxonomy and fisheries, Ricker was certainly an exception, and ideas and papers of contemporaneous entomologists impregnated his writings—thus, his famous paper describing stock-recruitment (Ricker 1954) was inspired by ‘the Nicholsonian point of view’ (Garfield 1982).

As *density-dependent* (qualifying a demographic mechanism or factor) turned to *density dependence* (representing a statistical relationship), *compensatory* and *depensatory* quickly became nominalized as *compensation* and *depensation* and have not resisted polysemy either. Thus, compensation is polysemous in population dynamics, most often associated with any ecological factor that takes over the role of others. As such, harvesting can compensate for DD mortality of target species (Heino and Dieckman 2008; Sinclair and Pech 1996), and more generally “...compensation is the demographic response to predation or harvest mortality ... usually due to density dependence” (Boyce et al. 1999). In examining tree canopy–gap formation, Clark (1992) defined *density compensation* as “...the degree to which mortality caused by density-independent factors is alleviated by reductions in density-dependent mortality”. Furthermore, Ricker (1958) borrowed body *growth compensation* from fisheries (Gilbert 1914; van Oosten 1928) and body *growth depensation* from Neave (1953): “Negative correlations [“increments in (body) size in successive years of life, among the fish of a given year-class”] indicate growth compensation, because they show that the smaller fish tend to catch up with the larger. Positive correlations

Table 2 Foundational terminology for the qualifiers of DD used in the modern literature of ecology, including the earliest terms coined to name each of four DD types, synonymous terms created by other authors (see references in Table 1) and population phenomena linked to those DD types in the ecological literature

| Qualifiers of density dependence/feedback ^a | | | Linked demographic phenomena | | | |
|--|---|--------------------------|--|------------------------------------|-----------------------|-----------------------|
| Earliest | Synonyms | Proposed | Crowding effect ^b on <i>r</i> , immigration, fertility, recruitment, survival | Emerging <i>N</i> dynamics | Population regulation | Population extinction |
| Direct (Allee 1941) | Compensatory/first-order/immediate/negative/self-thinning | Compensatory | Depression | Stability (dampening) | Yes | No |
| Delayed (Varley 1947) | Lagged/second-order ^c | Delayed compensatory | Depression | Stability (cycles) | Yes | No |
| Overcompensation (Varley et al. 1973) | Overcompensatory | Overcompensatory | Depression | Instability (chaos) | No ^e | Yes |
| Inverse (Allee 1941) | Allee effect ^d /depensatory/positive | Allee effect/depensatory | Enhancement | Instability ^d (decline) | No | Yes |

N, population size; *r*, overall population growth rate

^a Included are those qualifiers proposed in this study

^b Effects of opposite sign, from those reported in this column, are expected on emigration and mortality (Fig. 1)

^c Second-order DD implies a lag of two time steps, yet higher-order dynamics are possible (Berryman et al. 2002; Royama 1977)

^d Allee effects are a sort of depensation only at low population sizes (Courchamp et al. 1999). In theoretical scenarios, Allee effects have been shown to lead to population stability (Scheuring 1999), or to reduce the amplitude of oscillations (Fowler and Ruxton 2002)

^e Chaotic dynamics have been proposed to occur in the regulation of metapopulations (Allen et al. 1993; Hanski 1990)

have been called ‘reverse growth compensation’, but a shorter term might be ‘growth depensation’—adopting a word that was proposed in a different context by Neave (1954)” (year misquoted from 1953).

Positive and negative density-dependent

Haldane (1953) introduced the terms *negative density-dependent* and *positive density-dependent factors* to describe when overall population growth rates decrease or increase with population size, respectively (Table 1): “Smith called these density-dependent factors. It is perhaps better to call them negative density-dependent factors to distinguish them from [positive DD] factors, also dependent on density, which act in the opposite way, and make for instability”. Once more, Haldane synonymized *negative* with *direct* (Allee 1941) and *compensatory* (Neave 1953), and *positive* with *inverse* (Allee 1941) and *depensatory* (Neave 1953). Although Haldane (1953) did quote Varley and Allee, he ignored their older DD terms and remarked that negative DD could be *immediate* (=direct DD; Allee 1941) or *delayed* (=delayed DD; Varley 1947) (Tables 1, 2): “...the number of parasites emerging next year depends both on the number of hosts and that of parasites the year before, so control is delayed”.

In the modern literature, the terms *positive* and *negative* DD are often used to indicate the sign of a DD statistical relationship, irrespective of whether DD is compensatory or depensatory (contrary to Haldane’s terms), thereby provoking further polysemy. Thus, compensatory DD (theoretically

associated with population stability) equates both (1) to a negative relationship of population size with recruitment, reproduction, survival, immigration and/or population growth rates and (2) to a positive relationship of population size with mortality and/or emigration (Table 2; Fig. 1). The converse statistical signs hold for depensatory DD (theoretically associated with population instability) (Table 2; Fig. 1). The literature is plagued with examples that contradict Haldane’s (1953) lexicon. As an illustration, McCarthy (1997) wrote: “The Allee effect (negative density dependence) occurs when population growth rate is reduced at low population size (Allee 1931a, b, 1938)”, while Choi and Kimmerer (2008) wrote: “Mate limitation at low population levels can result in negative or depensatory density dependence, a form of positive feedback by which reproductive success declines as the population shrinks (Allee 1931a, b)”. Plant ecologists refer to *negative density dependence* (or *positive* for the opposite relationship) where dead individuals (e.g. trees) might have lower chances of being replaced by a conspecific if crowding exacerbates attack rates by specialized enemies, so facilitating the coexistence of common and rare species (Wright 2002).

Positive and negative feedback

In its simplest expression, a feedback occurs when the intensity of a factor affecting a system is modulated by the system itself via a reciprocal response or internal loop (see “Introduction”, ESM Fig. S1). The terms *negative feedback* and *positive feedback* originated from systems theory

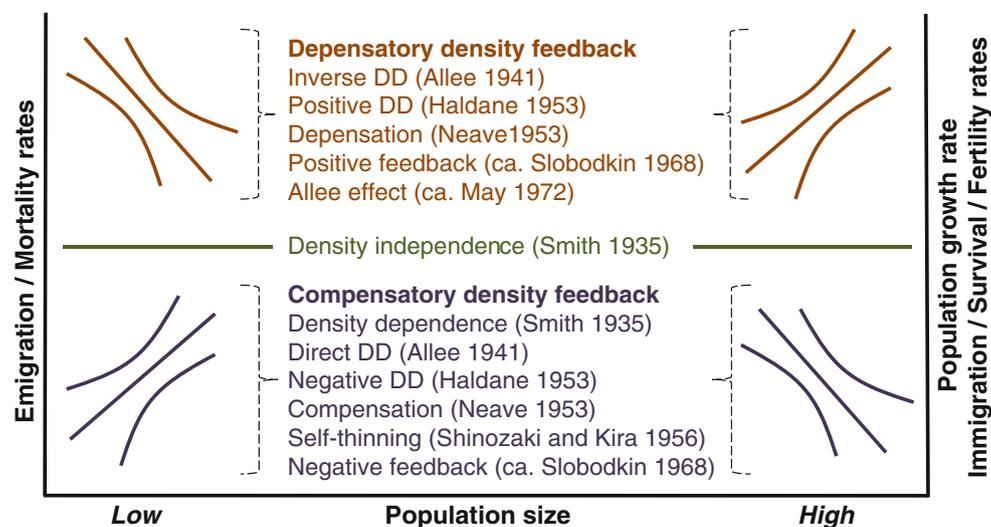


Fig. 1 Terminology mainly used in modern ecological literature to label contrasting depensatory and compensatory density feedbacks on different demographic rates (modified from Solomon 1976; see Tables 1, 2). For simplicity, we have used nominalized terms (e.g. *Depensation* for *Depensatory mortality factor*). Lines represent linear and nonlinear feedbacks. When authors name density feedback types

literally by the sign of the statistical relationship (i.e., *positive/negative* or *direct/inverse*), terms will potentially fall in conflict with original nomenclature. For instance, Haldane (1953) labelled compensatory feedback on any demographic rate as *negative density dependence*, but the positive relationship between population size and mortality (or emigration) rates also represents a compensatory feedback

which recognizes that natural, social and economic systems comprise groups of interacting entities governed by similar principles, however differently named per discipline (von Bertalanffy 1968). Feedback is one of those principles, its co-occurrence in machines and living organisms being the foundation of cybernetics (Wiener 1948). Wiener (1948) took the term feedback from the engineering sciences, and Milsum (1966) was among the earliest authors to relate it to population dynamics. The foundation of the term is certainly diffuse and can be frequently found before the 1970s in generic papers on biological systems (e.g. Dempster 1960; Manier 1970). The first authoritative usage of feedback terminology in population dynamics can be traced to Pimentel (1961, 1968), Slobodkin (1968) and Andrewartha (1970) and was much later rescued by Berryman (1989, 2002). Pimentel (1961) related mechanisms of *genetic feedback* with population regulation. Slobodkin (1968) overviewed different types of positive feedback in relation to changes in behaviour, evolution and demography: “...these alterations, in general, operate as feedback devices”, with no further reference to foundational nomenclature. This author had earlier commented on Nicholson’s cumbersome vocabulary (Slobodkin 1963). Interestingly and rarely cited, after denigrating DD in the 1950 and 1960s, Andrewartha (1970) partly restated the biological meaning of this concept using systems theory lexicon after considerably modifying one section in the second edition of one of his books (see his Fig. 9.10 classifying positive and negative feedbacks): “So much has been written about negative feedback (sic) to density in natural populations... I think that when the ecology of more species are known well density-dependent reactions will be found to be important in relatively few of them. This is not to deny that density-dependent reactions may occur in many ecologies and may prove to be important in some”. Recently, Kokko and López-Sepulcre (2007) defined an *ecogenetic feedback* whereby (evolution-based) life-history decisions cause population change and, in turn, (demography-based) density feedback shapes life-history selection.

Negative feedback is synonymous with *direct* (Allee 1941), *compensatory* (Neave 1953) and *negative* (Haldane 1953) DD, whereas *positive feedback* is synonymous with *inverse* (Allee 1941), *depensatory* (Neave 1953) and *positive* (Haldane 1953) DD (Table 2; Fig. 1). Many researchers conform to feedback nomenclature (e.g. Amarasekare 2004; Berryman 1989; Dornier et al. 2008; Holt 2009; Hunter 1998; McCarthy-Neumann and Kobe 2008; Rodenhouse et al. 1997; Tavecchia et al. 2007; Watson et al. 1998). However, feedback loops are not exclusive to demography, occurring in many biological (and non-biological) systems, whereas the terms *negative/negative feedback* are indistinctly used for genetic and demographic responses. Besides, they are also not safe from the

polysemous qualifiers presented above, such as *direct negative feedback* (Hofstetter et al. 2006; Lima et al. 2001).

Allee effect

This term refers to *depensatory* (Neave 1953) or *inverse* (Allee 1941) DD measured only at low population numbers (Courchamp et al. 1999) (Tables 1, 2). The origin of the expression *Allee effect* is mysterious across all DD jargon. For obvious reasons of humility, Allee did not brand the expression himself. It was Odum (1953) who labelled *Allee’s principle* only 2 years before the death of his colleague and *Allee growth type* later when describing the Allee effect graphically (Odum 1963) (Table 1). Odum’s linkage of Allee’s surname to a DD type seems crucial for the settlement of such a linkage thereafter. The question of who used *Allee effect* for the first time is still unresolved, but we have found it cited from the early 1970s onwards. When referring to it, authors (mis)quote either Allee’s earliest publications in the 1930 and 1940s or the four most cited (review) papers on Allee effects, namely those of Dennis (1989), Courchamp et al. (1999), Stephens and Sutherland (1999) and Stephens et al. (1999). These four reviews, and even a recent book devoted entirely to Allee effects (Courchamp et al. 2008), point towards *Allee’s principle* (Odum 1953) as the stepping stone to current lexicon, but they do not clarify the foundation of the term. We observe its first record as a note in small font at the end of May (1972): “...‘Allee effect’... whereby the per capita birth rate falls off at small x (population size). This result makes sense biologically: models incorporating the effect should permit the possibility of extinction” [therein *Allee effect* misquoted as Allee (1938)]. However, May has asserted that his work does not constitute the genesis of the term (R. May, personal communication).

In the ecological context, the steady extirpation of individuals at low population size can lead to extinction, while the steady addition of individuals can counteract the benefits of crowding, both effects potentially dismantling social organization. Allee effects are of obvious relevance to the conservation of populations and management of detrimental human impacts, being attributed to mechanisms such as failure of potential mates to encounter, collapse of social packing, inbreeding depression, demographic stochasticity (e.g. sex ratios), low fertility in threatened species and overharvesting (Berec et al. 2007; Courchamp et al. 2008; Gascoigne et al. 2009; Kramer et al. 2009; Stephens and Sutherland 1999) and by virtue of similar mechanisms, Allee effects are also applicable in pest and invasion control (Fagan et al. 2002; Tobin et al. 2011). Population growth models including Allee effects must be able to track a typically hump-shaped nonlinearity at the low spectrum of population sizes (Courchamp et al.

1999; Gregory et al. 2010; see associated terms in ESM Appendix 2).

Overcompensation

Varley created several modifiers for *compensation* by treating DD mortality relative to population return to carrying capacity: “The efficacy of a density dependent (sic) factor can be best considered in terms of compensation. Exact compensation is provided when a population (at density) N_0 above the equilibrium population (at density) N_e is brought down in a single step to that level” (Varley 1963). The entire idea fell within key-factor analysis, where the intensity of compensation was measured as the slope (β) of survivors [mathematically identical to the ‘instantaneous growth rate’ (Sibly and Hone 2002)] to logarithms of densities before mortality operated. So a population underwent *overcompensation* ($\beta > 1$), *exact compensation* ($\beta = 1$) or *under compensation* ($0 < \beta < 1$) when, following a population increase, a mortality factor brought numbers below, to or above carrying capacity, respectively (Varley and Gradwell 1970; Varley et al. 1973) (Table 1). This conceptualization stresses the fact that the magnitude of DD compensation must be quantified in response to proportional changes in population size (e.g. logarithmic scale) (Doncaster 2006, 2008), such as in the Gompertz model (see Table 3). Varley’s work pioneered the identification of thresholds of single-species population-model parameters relative to different population trajectories, overcompensation being from then on associated with population instability and chaotic phenomena (Hassell et al. 1976; Hastings 2009) and mechanisms such as scramble competition in response to limited resources (Bellows 1981). A recent food-addition experiment showed that, irrespective of low or high nutrient availability, stochastic provision of beans to beetle populations shifted the strength and shape of DD and triggered remarkably wider population fluctuations compared to controls with regular food provision (Bull and Bonsall 2008). Those authors defined *overcompensation* as “...a nonlinear density dependence leading to populations overshooting equilibrium” (with no reference to Varley’s seminal work and terms).

Overcompensation has also succumbed to polysemy. Botanists and fish ecologists use *compensation* and *overcompensation* to label different degrees of nonlinearity of density feedbacks. Thus, *overcompensating negative density dependence* refers to a steep nonlinear decline in plant recruitment as seed density increases across several sites (Bagchi et al. 2010; Freckleton and Lewis 2006), whereas *overcompensation* also relates to pronounced declines in fish recruitment across stocks from low to high spawner abundances (Bjorkstedt 2000; Myers 2001). In a different context, *overcompensation* means a human-induced feedback

where fishing pressure magnifies stock size by (1) promoting sex inversion (Beentjes and Carbines 2005), or (2) increasing juvenile (*reproduction regulation*) or adult (*maturation regulation*) biomass through stage-specific demographic responses (de Roos et al. 2007; Zipkin et al. 2008). Moreover, plant demographers commonly describe individuals that overcompensate for herbivory through increasing branching and fruit and seed production (Belsky 1986).

Simple rules of nomenclature

The biography of DD terms reveals five reasons why this terminology has become inconsistent. Firstly, ecologists who forged the DD concept appointed terms from their own areas of expertise, often ignoring (deliberately or unintentionally) those of their colleagues in the same (e.g. entomology) and different (e.g. botany, ecology, fisheries, zoology) disciplines. Secondly, from the earliest to modern DD literature, polysemy reveals carelessness among authors to check the correct semantics of their lexicon with regard to the original nomenclature, a problem that is spread throughout the ecological literature (Todd and Ladle 2008; Todd et al. 2007) given the enormity of the knowledge base which now exists. Thirdly, experts have furnished new terms to ground their views in debates about the biological meaning of DD and demographic role of DD mechanisms, and how to provide statistical evidence for that role, particularly relative to population regulation (Cooper 2001; Murray 1982; Royama 1977; Sale and Tolimieri 2000). Fourthly, modern ecologists work in different philosophically based paradigms to study population dynamics (Krebs 2002b), and the semantic range of lexicon overlaps across those paradigms. Lastly, research progress leads to new lexicons as the understanding of concepts is refined, as illustrated by Allee effects (Berec et al. 2007). We expand these points in the ESM (Appendix 2), featuring further ramifications of the DD lexicon as a result.

We acknowledge that “...language seldom changes by prescription” (Hodges 2008), and it might be unrealistic to attempt to change current DD nomenclature habits (however necessary this might be) strengthened by nearly a century of usage. Nevertheless, we hope to encourage ecologists by suggesting that much terminological inconsistency can be overcome by applying three simple rules that are rigorous with respect to the biological meaning of DD.

Rule 1: *Density feedback* is semantically more precise than *density dependence*

Density dependence evokes a correlation, *density feedback* recreates the causality inherent in the concept DD;

therefore, *density feedback* is a better term (Berryman 1989; Berryman et al. 2002). Berryman et al. (2002) advocated changing from *density dependence* to *density feedback*, yet forecast correctly that: “Many ecologists... will disagree with our recommendation that the traditional terminology be abandoned”. The choice between the two expressions is semantic and does not cause terminological ambiguity.

Rule 2: *Compensatory* and *depensatory density feedbacks* are independent of the sign of statistical relationships

The DD vocabulary has attempted to discriminate two broad types of density feedback, whether the effect of increasing population size on a demographic rate contributes to either enhancing or arresting a population’s overall rate of growth (Table 2; Fig. 1). The qualifiers *compensatory* and *depensatory* (Neave 1953) density feedback (or *compensation* and *depensation*) make such distinction neatly (e.g. Rose et al. 2001), circumventing terminological ambiguities to name the sign of DD statistical relationships.

It is equally important to acknowledge the following. Firstly, *Allee effects* are a form of depensatory feedback occurring only at low population numbers, so not all depensation matches an Allee effect. Secondly, when assessing the order of compensatory density feedback, *immediate* and *delayed* (Haldane 1953) identify feedbacks between consecutive or longer time steps, respectively; systems theory provides the qualifiers to name unequivocally the number of time steps involved, such as *first-order* and *second-order*, which equal immediate and delayed (with two time steps) compensatory density feedback, respectively. Thirdly, when measures of strength of density feedback are linked to measures of temporal variance of population size, *undercompensatory* and *overcompensatory* (Varley et al. 1973) density feedback separate population stability from instability, respectively. However, the thresholds of density-feedback strength, distinguishing contrasting dynamics, will be model-dependent, as May (1974, 1976) exemplified for simple demographic models. We caution that the meaning of (*over/under*) *compensatory* feedback has been split within three different theoretical frameworks of demography, namely, (1) temporal population dynamics (population-size predictor N = density over a sequence of times), (2) plant-species coexistence (N = seed/seedling/adult density at different sites) and (3) fishery stock-recruitment models (N = spawner density at different stocks), which has in turn pumped new DD terms, such as *symmetric* (Volkov et al. 2005) and *asymmetric* (Comita et al. 2010) *density dependence*, into the lexical balloon. This partly indicates terminological friction between temporal and spatial population demography,

which needs cross-discipline revision beyond the scope of our review.

In summary, five DD qualifiers (*compensatory*, *delayed compensatory*, *overcompensatory* and *depensatory/Allee effects*) seem necessary to describe four population phenomena that might be theoretically linked to the action of density feedbacks, namely dampening, cycles, chaos and decline (Table 2; ESM Appendix 3).

Rule 3: *Ensemble density feedback* encapsulates the interplay of components of density feedback

Stephens et al. (1999) coined the terms *component Allee effects* when measured on single demographic rates (components of total fitness), and *demographic Allee effects* when measured on the overall rate of population growth (total fitness). We suggest that this terminological distinction is routinely employed by ecologists to report both depensatory and compensatory density feedbacks. However, we favour the qualifier *ensemble* over *demographic* because *ensemble density feedback* ingrains the notion that the overall density effect on a population’s growth rate is the synthesis of all component feedbacks on single demographic rates (Herrando-Pérez et al. 2012)—whereas *demographic density feedback* might be confused with *component density feedback* operating on *demographic* rates. Note that *ensemble* and *component* density feedbacks do not refer to the sign of DD relationships, so both can therefore be compensatory or depensatory, while *ensemble Allee effects* will be synonymous with Stephens et al.’s (1999) *demographic Allee effects* (Table 1).

The conceptual (hence terminological) distinction of component and ensemble feedbacks has essential implications in the way ecologists relate DD measurements to population dynamics and resulting management and conservation actions. Essentially, unless component feedbacks are measured on all relevant demographic rates of a population (a nearly impossible task even for the best-studied populations), finding statistical evidence for single component feedbacks is no guarantee that an ensemble feedback exists or can be measured, or that various phenomena, such as population regulation, emerge from component feedback (Herrando-Pérez et al. 2012)—a common inference in the ecological literature (e.g. Gough and Kerley 2006; Pistorius et al. 2008; Pöysä and Pesonen 2003). According to Sinclair and Pech (1996), *regulation* entails that the effect of all component compensatory feedbacks must exceed that of all component depensatory feedbacks (‘net density dependence effect’). So in theory, a suite of component compensatory and depensatory feedbacks [see Berec et al. (2007) for *multiple Allee effects*; Bjorkstedt (2000) for *concurrent* DD] can act simultaneously on reproduction, survival and dispersal rates. Kolb et al.

Table 3 Sample of popular tests for DD in censuses of population abundance

| Reference | Statistic | Statistic source | Models | Outcome thresholds |
|--------------------------------------|---|--|---|---|
| Moran (1953) | ρ (serial correlation, lag k) | p value table | $\rho[N_{t+k}, N_t]$ for all t | $H_0: \rho = 0 \rightarrow$ DI $H_1: \rho \neq 0 \rightarrow$ (delayed if $k > 1$) DD |
| Tanner (1966) | ρ (correlation) | p value table | $\rho\left[\frac{N_{t+1}-N_t}{N_t}, N_t\right]$ for all t | $H_0: \rho = 0 \rightarrow$ DI $H_1: \rho \neq 0 \rightarrow$ DD |
| Varley (1963) | t -student (regression) | p value table | (0) Random walk $r = \varepsilon_t$ (1) Linear regression ^a $r = \beta X_t + \varepsilon_t$ | $H_0: \beta = 0 \rightarrow$ DI $H_1: \beta \neq 0 \rightarrow$ DD |
| Bulmer (1975) | R (\sim serial correlation, lag 1) R^* (\sim serial correlation, lag k) | Simulation | (0) Random walk $X_{t+1} - \mu = (X_t - \mu) + \varepsilon_t$ (1) Density dependence $X_{t+1} - \mu = \beta(X_t - \mu) + \varepsilon_t$ | $H_0: \beta = 1 \rightarrow$ DI $H_1: \beta < 1 \rightarrow$ (delayed if $k > 1$) DD |
| Pollard et al. (1987) | T or r_{dx} (0,1) (LR) T or r_{dx} (0,2) (LR) T or r_{dx} (1,2) (LR) | Randomization | (0) Random walk $X_{t+1} = X_t + \varepsilon_t$ (1) Random walk with drift $X_{t+1} = d + X_t + \varepsilon_t$ (2) Density-dependence $X_{t+1} = d + \beta X_t + \varepsilon_t$ | $H_0: d = 0, \beta = 1 \rightarrow$ DI $H_1: d \neq 0, \beta = 1 \rightarrow$ DI $H_2: d \neq 0, \beta \neq 1 \rightarrow$ DD (Pair-wise contrasts) |
| Dennis and Taper (1994) ^b | T_{01} (LR) T_{02} (LR) T_{12} (LR) | Parametric bootstrapping | (0) Random walk $X_{t+1} = X_t + \varepsilon_t$ (1) Random walk with drift $X_{t+1} = d + X_t + \varepsilon_t$ (2,2 _a ,2 _b) Stochastic logistic $X_{t+1} = d + X_t + \beta e^{X_t} + \varepsilon_t$ | $H_0: d = 0, \beta = 0 \rightarrow$ DI $H_1: d \neq 0, \beta = 0 \rightarrow$ DI $H_2: d \neq 0, \beta \neq 0 \rightarrow$ DD $H_{2a}: d \neq 0, \beta < 0 \rightarrow$ CDD $H_{2b}: d \neq 0, \beta > 0 \rightarrow$ DDD (Pair-wise contrasts) |
| Brook and Bradshaw (2006) | wt DD (Multi-model inference) | Akaike's information criterion adjusted for finite sample size (AIC _c) | (0) Random walk $r = \varepsilon_t$ (1) Exponential $r = r_m + \varepsilon_t$ (2) Ricker-logistic $r = r_m \left[1 - \left(\frac{N_t}{K}\right)\right] + \varepsilon_t$ (3) Theta-logistic $r = r_m \left[1 - \left(\frac{N_t}{K}\right)^\theta\right] + \varepsilon_t$ (4) Gompertz ^a $r = \beta X_t + \varepsilon_t$ | $M_0: r_m = 0 \rightarrow$ DI $M_1: r_m \neq 0, \theta = -\infty \rightarrow$ DI $M_2: r_m \neq 0, \theta = 1 \rightarrow$ DD $M_3: r_m \neq 0, \theta \neq 1 \rightarrow$ DD $M_4: \beta \neq 0 \rightarrow$ DD (Multi-model contrast: wt DD = $wAIC_{c-M2} + wAIC_{c-M3} + wAIC_{c-M4}$) |

All models equate population size at time $t + 1$ (alone or combined with other terms) (response) against population size the previous time point t (predictor). Time points vary among studies that have applied those tests (e.g. days, months, seasons, years and generations)

Variables: t , time; N , population size; X , $\log_e(N)$; r , $\log(N_{t+1}-N_t)$, overall population growth rate; d , drift parameter

Constants: μ , mean(X) (equilibrium); a, b , constants; K , carrying capacity; r_m , maximum growth without DD

Methods: LR, likelihood ratio; $wAIC_c$, model weight; wt DD, $\Sigma wAIC_c$ for DD models: $\Sigma wAIC_c$ for DD + DI models = 1

Evidence: \rightarrow DI, density independence; \rightarrow (C/D) DD, (compensatory/depensatory) density feedback

^a Gompertz model (Medawar 1940; Nelder 1961)

^b Dennis and Taper (1994) used a stochastic logistic model (shown), and a stochastic Gompertz model

(2010) found depensatory density feedback on single demographic rates (e.g. potential seed production) of a rare perennial herb that had no effect on its population growth rate and alerted researchers to the fact that: "...we need to be cautious when assessing the consequences of habitat fragmentation for population viability based on (density) effects on only one or a few vital rates". Likewise, we (Herrando-Pérez et al. 2012) have recently identified decoupling of component and ensemble density feedbacks in >100 populations of birds and mammals, drawing the conclusion that "...the management of anthropogenic impacts on populations using component feedbacks alone

is ill-advised, just as managing on the basis of ensemble feedbacks without a mechanistic understanding of the contributions made by its components and environmental variability can lead to suboptimal decisions".

Density feedback and population regulation are not the same

Density dependence measurements of any kind (i.e. statistical evidence, strength or shape of both component and ensemble density feedback) do not imply population

regulation. DD contributes to principles in crucial areas, such as ecosystem services, population viability or harvest quotas, but linking those tenets conceptually to population regulation only through a DD metric/model is potentially flawed (e.g. Bohan et al. 2011; Brook and Bradshaw 2006; Henle et al. 2004; Sibly et al. 2005). In essence, compensatory density feedback is one of the statistical requirements of—but not a test for—regulation; hence, the plain statements that density feedback “...is necessary but not sufficient for population regulation” (Hixon et al. 2002; Turchin 1995), and “...the necessary and *sufficient* condition for regulation in a population model is the presence of negative feedback *and* parameter values that allow the population to persist”. We agree with Krebs (1995) that “...most ecologists now seem to assume that the proper approach to population regulation is through density dependence, and the two terms regulation and density dependence (our emphasis) are virtual synonyms in much of the current literature”.

We attribute this historical confusion to three reasons. Firstly, the quest for population regulation over most of the second half of the twentieth century was subordinate to the development of continuously evolving DD tests (e.g. Fox and Ridsdillsmith 1995; Freckleton et al. 2006; Hassell 1986; Holyoak and Lawton 1992; May 1989; Wolda et al. 1994) (Table 3); therein, seeking evidence for DD was often implicitly meant also to be evidence for regulation: “Many populations appear to fluctuate about an equilibrium value ... such a population is said to be density dependent or regulated” (Bulmer 1975) (see below). Secondly, the recent turn from DD testing to modelling (Bjørnstad and Grenfell 2001) makes DD parameters implicit in mathematical equations (although not necessarily biologically meaningful, Clark et al. 2010), which might theoretically account for population regulation—so again, with one stroke, statistical evidence for a given model is assumed to bring about joint evidence for both DD and population regulation (e.g. Ziebarth et al. 2010). Thirdly, both the conceptual and mathematical definitions of the concept *population regulation* remain to be unified, which is exemplified by Murdoch’s (1994) droll observation that “...regulation seems best defined by defining non-regulation”.

For some authors, the existence of an *equilibrium* (or *carrying capacity*) and a *return tendency* (i.e. through the operation of a factor driven by compensatory density feedback) are the key elements for population regulation, thus, the definition “...return tendency of a population to equilibrium density” (Murdoch 1970) or “...presence of a long-term stationary probability of population densities... if we define equilibrium broadly as a stationary probability distribution, then being regulated and having an equilibrium are one and the same thing” (Turchin 1995); however, detractors have questioned the difficulty of interpreting

what this equilibrium means in nature (Berryman 1991; Wolda 1989). Nevertheless, the former definitions certainly harmonize with DD tests and models that incorporate some measure of equilibrium, be they stochastic [as in Dennis and Taper’s (1994) parametric-bootstrap likelihood-ratio test, Crowley’s (1992) density-attractor test or sophisticated models such as ARMA (Ives et al. 2010)] or fixed [e.g. equilibrium = average $\log_e(N_t)$ in Bulmer’s (1975) test, or the magnitude of evidence for logistic models as assessed using information-theoretic approaches (Brook and Bradshaw 2006)] (Table 3).

Other authors invoke several phenomenological properties such that “...by definition, a population is regulated when it displays three closely related phenomena: (1) persistence, (2) boundedness, and (3) return tendency” (Hixon et al. 2002), which have also encountered opposition in that “...interpretations which equate regulation with persistence of populations (Hanski 1990; Krebs 1995; Reddingius and den Boer 1989) merely lead to confusion” (Sinclair and Pech 1996), as well as a gamut of rival concepts as a result of incorporating spatial structure into population models, such as *spreading the risk* (den Boer 1968) and *stabilization* (den Boer 1986), *vagueness* (Strong 1986), *metapopulation regulation* (Hanski 1990), *site-dependent regulation* (Rodenhouse et al. 1997), *determination* (Sale and Tolimieri 2000) and *limitation* (White 2001). These all represent the friction of terminology between temporal and spatial demography. These debates resurrected the popular exchanges between Nicholson and Andrewartha (Andrewartha 1958, 1959; Nicholson 1958, 1959), but are currently dormant. Meanwhile, to characterize when a population is regulated, it remains unclear what needs to be measured, how it should be measured and even whether the measurement is of any use. The common use of the expression *density-dependent regulation* firms up the marriage of both concepts and disregards that (see Hassell et al. 1976): “The detection of density dependence will not, in itself, prove that regulation is occurring, since the density-dependent response must be of the right form and size if it is to be capable of damping fluctuations in population size” (Dempster 1983) (Table 2).

Conclusions

Ecology is a realm of scientific enquiry still to make a reputation for lexical standards (Adams et al. 1997; Hodges 2008; Whittaker 1957), where context-specific comprehension of terminology (i.e. within single publications) seems to be taken as the silent rule, regardless of consistency across the literature. Experts with a strong numerical background will surely argue that theoretical models define ecological concepts accurately in the universal and

unambiguous language of mathematics, thus dispensing with the need for standardizing terminology. However, sound statistical expertise belongs to a minority of ecologists and biologists (Johnson et al. 2001), such that mathematical language will not improve communication in our field until education providers improve the quality of statistical training at the earliest undergraduate and postgraduate stages. Further, scientific papers are written in (mostly) English, not entirely with equations. Meanwhile, it is hardly conceivable that mathematics has bettered the understanding of DD among ecologists; rather, we argue the contrary. We concur with Krebs (1995) that this concept owes popularity among ecologists to its amenability to mathematical treatment. As a result, DD models have become increasingly complex (Clark et al. 2010), and "...a serious drawback is that almost all such models are truly understood only by those who do the actual construction of a given model, and readers of reports on the results have to take a lot on faith" (Eberhardt et al. 2008).

The pace of progress of ecological knowledge does not follow the pace of review, updating and even the creation of new terminology, which leads directly to terms acquiring polysemy and synonymy. Among the >60 terms of DD, foundational terminology by Smith, Allee, Varley, Neave and Haldane is still in use, but its meaning is often not respected, miscited relative to original literature or incorrectly equated with *population regulation*. Historically, controversial concepts, such as DD, face unavoidable semantic inflation, as authors debate theoretical and empirical aspects fundamental to those concepts. Each scientist can defend a different definition of ecological concepts, but this will inevitably trigger polemics that overemphasize individual points of view at the expense of general understanding. Importantly, students and early-career researchers will be challenged by those concepts if the very experts from whom they take instruction disagree in their terminology and definitions.

A gradual unification of the nomenclature of ecology, currently fragmented by disciplines and strongly opinionated schools of thought (as exemplified by the history of DD; Krebs 2002b), could ameliorate the classification scheme of ecological knowledge. Journals could improve terminological standards by featuring permanent sections uniquely focussing on the review of terminology and by enforcing guidelines whereby authors are not able to invent new definitions but instead must authorize the foundational ones. In addition, the entire field of ecology would benefit enormously if a *Journal of Ecological Nomenclature* was created. Terminology represents one of those matters about which many voices complain, but provide no solution. The establishment of regulatory rules for ecological terminology (once attempted by the Ecological Society of America;

Eggleton et al. 1952; Hanson et al. 1931) is condemned a priori to be an unpopular idea for many scientists. Yet it is already taken as a self-evident necessity in many diverse fields, such as astronomy, chemistry, genetics, medicine or taxonomy. If words were taxa, one can imagine the herculean enterprise of reviewing an entire taxonomic family consisting of tens of different genera and species (of words) bearing etymology subject to no rules—the ecological literature is exemplary in the frequency of such semantic chameleons (e.g. *carrying capacity*, *niche*, *population regulation*, *species*). Certainly, terminology is the key for communication and merits more respected recognition in ecology.

Finally, ecologists are increasingly interacting with society through policy-makers, management and conservation planners and the media (Adams et al. 1997; Murphy and Noon 1991; Weber and Word 2001). There, scientific discourse becomes a tool of communication with non-scientists, and clear terminology is instrumental to important matters, such as the attraction of research funding and precise conveyance of scientific information for societal benefit. Social abilities are now needed and, among them, a dosage of linguistics and philosophy is perhaps missing in the curricula of skills of modern ecologists. A reflection has been put forward elsewhere that "...the ecological approach to language requires a considerable amount of unlearning or re-evaluation of existing linguistic knowledge" (Mühlhäusler 2003)—as Elton (1950) satirized: "We have to be prepared for an insistence on philosophical definition of terms and concepts which makes the average empirical British ecologist feel rather as if he were having all his familiar old clothing removed by stages for cleaning and pressing". Yet terminology is important, but not a panacea: "The next generation of ecologists must be prepared to interact with such disciplines as history, religion, philosophy, geography, economics and political science. The requisite training must involve not only words, but core skills in these disciplines" (Ludwig et al. 2001).

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