

Current Usage of Symbiosis and Associated Terminology

Bradford D. Martin^{1,2} & Ernest Schwab¹

¹ School of Allied Health Professions, Loma Linda University, Loma Linda, CA, USA

² Department of Biology, La Sierra University, Riverside, CA, USA

Correspondence: Bradford D. Martin, School of Allied Health Professions, Loma Linda University, Loma Linda, CA 92350, USA. Tel: 1-909-558-4632. E-mail: bdmartin@llu.edu

Received: October 8, 2012 Accepted: November 1, 2012 Online Published: November 29, 2012

doi:10.5539/ijb.v5n1p32

URL: <http://dx.doi.org/10.5539/ijb.v5n1p32>

Abstract

Confusion has afflicted the definition of *symbiosis* for over 130 years. Despite the lack of discussion in recent times, the usage of symbiosis has evolved and appears to be stabilizing to broader interpretations. Current usage of symbiosis and its associated terminology in 10 current general biology (GB) and 10 general ecology (GE) textbooks is presented. The restrictive definition (i.e. symbiosis = mutualism) has essentially disappeared. All GB textbooks (100%) surveyed used an explicit or implicit “de Bary” definition of symbiosis (i.e. mutualism, commensalism, and parasitism), while only 40% of GE textbooks did the same. General ecology textbooks also included 30% defining symbiosis to constitute all species interactions and 30% that completely avoided usage of the term. When combining GB and GE textbooks to analyze symbiotic usage, 85% defined mutualism, commensalism, and parasitism as symbiotic interactions. Also, 70% considered a symbiosis to be a species interaction that is “intimate,” with 45% of those both “intimate and constant.” Unfortunately, only 5% used the terms *ecto-/endosymbiosis*, which help discern intimacy and constancy in species interactions. Usage of *symbiont* (55%) was preferred over *symbiote* (0%). Predator and prey were defined as organisms (vs. animals) in 90% of GB and GE textbooks, while 55% and 75% described *carnivores* and *herbivores* as organisms, respectively. Only 25% discussed predation, parasitism, parasitoidism, and grazing/herbivory, with only one (5%) integrating these +/- *agonistic* interactions in relation to intimacy and lethality. Data reveals trend of biologists/ecologists using broader definitions.

Keywords: symbiosis, symbiotic terminology, confusion, species interactions, predation, carnivory, herbivory

1. Introduction

...*symbiosis is such a universal and important phenomenon that it should be an integral component of the education of biologists.* – Ahmadjian and Paracer (1986).

Symbiosis has probably created the greatest quandary in the history of biological terminology. No other term has experienced as much confusion, variation in definition, and controversy (Starr, 1975; Lewis, 1985; Saffo, 1992; Douglas, 1994; Sapp, 1994; Paracer & Ahmadjian, 2000; Wilkinson, 2001; Moran, 2006; Martin & Schwab, 2012). It has endured misuse and confusion for over 130 years, ever since Anton de Bary (1879) coined the word. However, Sapp (1994) contends that Albert Bernhard Frank actually coined the word in 1877. Despite whoever coined the word and the prolonged confusion in the various meanings, it continues to be used today, indicating its importance and centrality in describing symbiotic phenomena (Stock et al., 2010). A few biologists would argue that the confusion will never be resolved and that we must learn to define the term whenever it is used (Hertig, Taliaferro, & Schwartz, 1937; Whitfield, 1979; Bronstein, 1994; Wilkinson, 2001) or not to be concerned with multiple definitions (Whitfield, 1979; Lewin, 1982). Around 1960-1990, some biologists believed that the common restrictive definition (i.e. symbiosis = mutualism) had replaced de Bary’s original definition (i.e. symbiosis = mutualism, commensalism, and parasitism) (Scott, 1969; Whitfield, 1979; Lewin, 1982; Trager, 1986). Furthermore, Pianka (2000) modified this definition of symbiosis to include species interactions wherein neither species is harmed (i.e. mutualism, commensalism, and neutralism). Ironically, this non-parasitological consensus, if it did exist, has almost completely vanished from the literature of the 2000’s (Martin & Schwab, 2012).

To add to the confusion of symbiosis proper, there is also a substantial amount of unintentional chaos in secondary term usage (e.g. variation in definitions of parasitism and commensalism, less common terms such as

phoresy and inquilinism, use of symbiont vs. symbiote, and use of predatory/carnivory/herbivory) that has further diverted biologists from solidarity on the main term. This muddle and confusion may persist indefinitely to confound and exasperate biologists who desire a consensus in utilizing symbiotic terminology. The controversy over definition has been debated so much that several authors of current general ecology textbooks (Krohne, 2001; Molles, 2010; Miller & Spoolman, 2012) have completely avoided usage and discussion of the term symbiosis. This is unfortunate because there is a need for a word to unite our understanding of species interactions and coevolutionary ideas.

Many broad and narrow interpretations have been previously proposed or used in hopes of reducing confusion (Martin & Schwab, 2012). However, the restrictive interpretations have been extremely perplexing to the biologists whose research areas are not included in the narrowly focused usages. Very broad perspectives were formally proposed over the years (McDougall, 1918; Starr, 1975; Lewis, 1985) and other authors, mostly recent, have also expressed an innate understanding that symbiosis should include much more than the traditional de Bary definition (Hegner, 1929; Cooke, 1977; Kormondy, 1996; Odum & Barrett, 2005; Krebs, 2009; Sharma, 2009; Peacock, 2011). Also, no other word has been proposed or currently exists that could fill the verbal niche that incorporates all the various types of species interactions. Researchers are discovering that symbiosis is central to our understanding of most, if not all, areas of ecology and biology (Peacock, 2011). However, it is still unclear what types of species interactions should be included under the umbrella of symbiosis. Many authors have noted this confusion and/or have attempted to address the problems and propose solutions to reduce the confusion as to which interactions are considered symbiotic (Pound, 1893; McDougall, 1918; Odum, 1971; Starr, 1975; Richardson, 1977; Lewis, 1985; Trager, 1986; Saffo, 1992; Smith, 1992; Bronstein, 1994; Douglas, 1994; Wilkinson, 2001; Moran, 2006). A trend of broadening the definition of symbiosis in the de Bary sense has occurred around the 1990's (Margulis, 1990; Saffo, 1992; Bronstein, 1994; Starr & Taggart, 1992; 1998), resulting from the realization that mutualism, commensalism, parasitism, and predation are all part of a continuum of species interactions (Douglas & Smith, 1989; Guttman, 1999).

All desire a universal resolution of the term, but no proposals, thus far, have been convincing or practical enough to gain wide acceptance and adoption in usage. Relatively few articles in the primary literature have addressed the confusion issue in the past 15 years (Wilkinson, 2001; Sapp, 2004; Peacock, 2011). However, despite this lull in the definition debate, textbook approaches to symbiosis have been evolving devoid of any official recommendations by biological associations. This review presents the current usage of symbiosis and its associated terminology in general biology and general ecology textbooks. This is the first publication to quantify symbiotic term usage, for either textbooks or primary literature. Awareness of how entry-level textbooks are preparing future biologists in the early 2000's is very important in facilitating how the term will be used for all biologists during the remainder of this century.

2. Methods

Current and popular general biology (GB) and general ecology (GE) textbooks were thoroughly examined to qualify and quantify how biological authors use and define symbiosis and its associated terminology. These were current editions of GB (n=10) and GE (n=10) textbooks with mean publication dates of 2010.6 ± 0.7 and 2007.2 ± 3.4 , respectively. The more recent mean publication date for GB textbooks can be attributed to the higher competition between publishers for the lucrative sales volume of GB, relative to GE textbooks. All GB and GE textbooks were college-level, except for one popular high school GB textbook included as a reference (Miller & Levine, 2010). The mean edition number for GB textbooks was 6.7 ± 4.0 and GE textbooks was 5.4 ± 2.2 . Six of the GB textbooks were in 9th-12th editions and therefore are well-established textbooks. Conversely, 3 of the 10 GB textbooks were in 1st or 2nd editions to add fresh and newer perspectives to symbiotic terminology. The GB textbooks included Starr, Taggart, Evers, and Starr (2009), Mader (2010), Miller and Levine (2010), Brooker, Widmaier, Graham, and Stiling (2011), Freeman (2011), Raven, Johnson, Mason, Losos, and Singer (2011), Reece et al. (2011), Russell, Hertz and McMillan (2011), Sadava, Hillis, Heller, and Berenbaum (2011), and Solomon, Berg, and Martin (2011), while GE textbooks included Krohne (2001), Bush (2003), Odum and Barrett (2005), Begon, Townsend, and Harper (2006), Ricklefs (2008), Krebs (2009), Sharma (2009), Smith and Smith (2009), Molles (2010) and Miller and Spoolman (2012). All textbooks were examined for terminology usage in glossaries, as well as in chapters where terms were defined and elaborated. When discrepancies existed between glossary and chapter definitions, usage in the broader sense (i.e. organism, rather than animal/plant) was reported. A chi square test for heterogeneity was run to determine any significant differences between GB and GE textbook categories in how they define symbiosis.

3. Results

Only one of the GB and GE textbooks (5%) cited Anton de Bary as the first biologist to propose the term symbiosis and also discussed the confusion that exists in the literature (Sharma, 2009). However, 80% of GB textbooks explicitly utilized de Bary's definition, while 20% implied a modified de Bary definition, which includes parasitoidism (Figure 1). The latter two textbooks explicitly discussed mutualism and parasitism as being symbiotic, but implied commensalism and parasitoidism by stating symbiosis is "an intimate association between two or more organisms of different species" (Brooker et al., 2011) or "the living together of two or more species in a prolonged and intimate relationship" (Sadava et al., 2011). None of the GB or GE textbooks used the restrictive definition (i.e. symbiosis = mutualism). General ecology textbooks exhibited high diversity in defining symbiosis and were significantly different ($P < 0.001$) than GB textbooks (Figure 1). Only one GE textbook (10%) used an explicit de Bary definition and 30% utilized a modified de Bary definition as described above. Another 30% defined symbiosis as all species interactions, while 30% completely avoided using symbiosis throughout the entire textbook (Figure 1). Technically, four GE textbooks (40%) recognized two definitions of symbiosis (not shown in graphs, with three of these defined in glossary): All four recognized the restrictive definition, but utilized broad definitions in text chapters (i.e. one used a de Bary definition and three used symbiosis = all interactions).

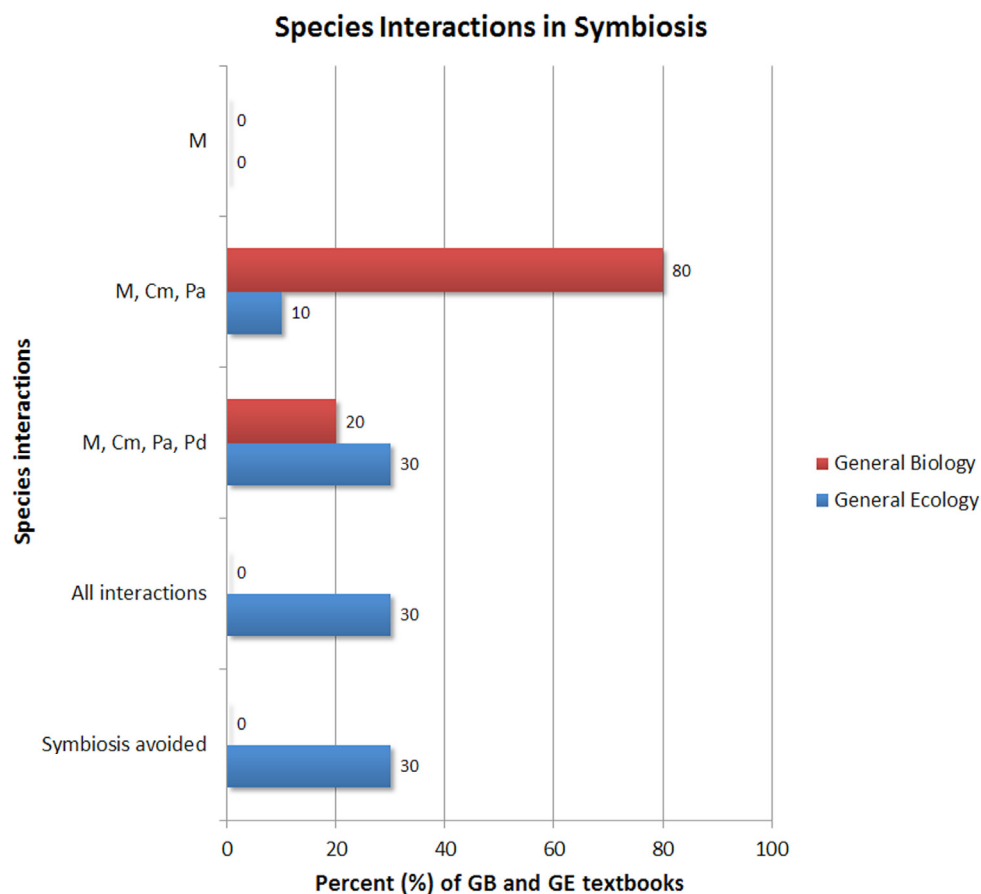


Figure 1. Percent of various combinations of species interactions defined as a symbiosis by current general biology (GB) and general ecology (GE) textbooks

M = mutualism; Cm = commensalism; Pa = parasitism; Pd = parasitoidism. All interactions include M, Cm, Pa, Pd, as well as neutralism, amensalism, competition, grazing, predation, phoresy, facilitation, and protocoeperation. Three GE textbooks (30%) avoided using *symbiosis* entirely.

When combining all 20 GB and GE textbooks to analyze symbiotic usage, 85% defined mutualism, commensalism, and parasitism (i.e. de Bary's definition) as symbiotic interactions (Figure 2). *Parasitoidism* is

often considered symbiotic and 35% of these textbooks included this species interaction (Figure 2). Commensalism was described as very similar to mutualism and parasitism in 20% and 15% of GB and GE textbooks, respectively, and difficult to discern the differences. When analyzing all the remaining species interactions, 15% of GB and GE textbooks (all of which were GE textbooks) considered all species interactions to be symbiotic (Odum & Barrett, 2005; Krebs, 2009; Sharma, 2009) (Figure 2).

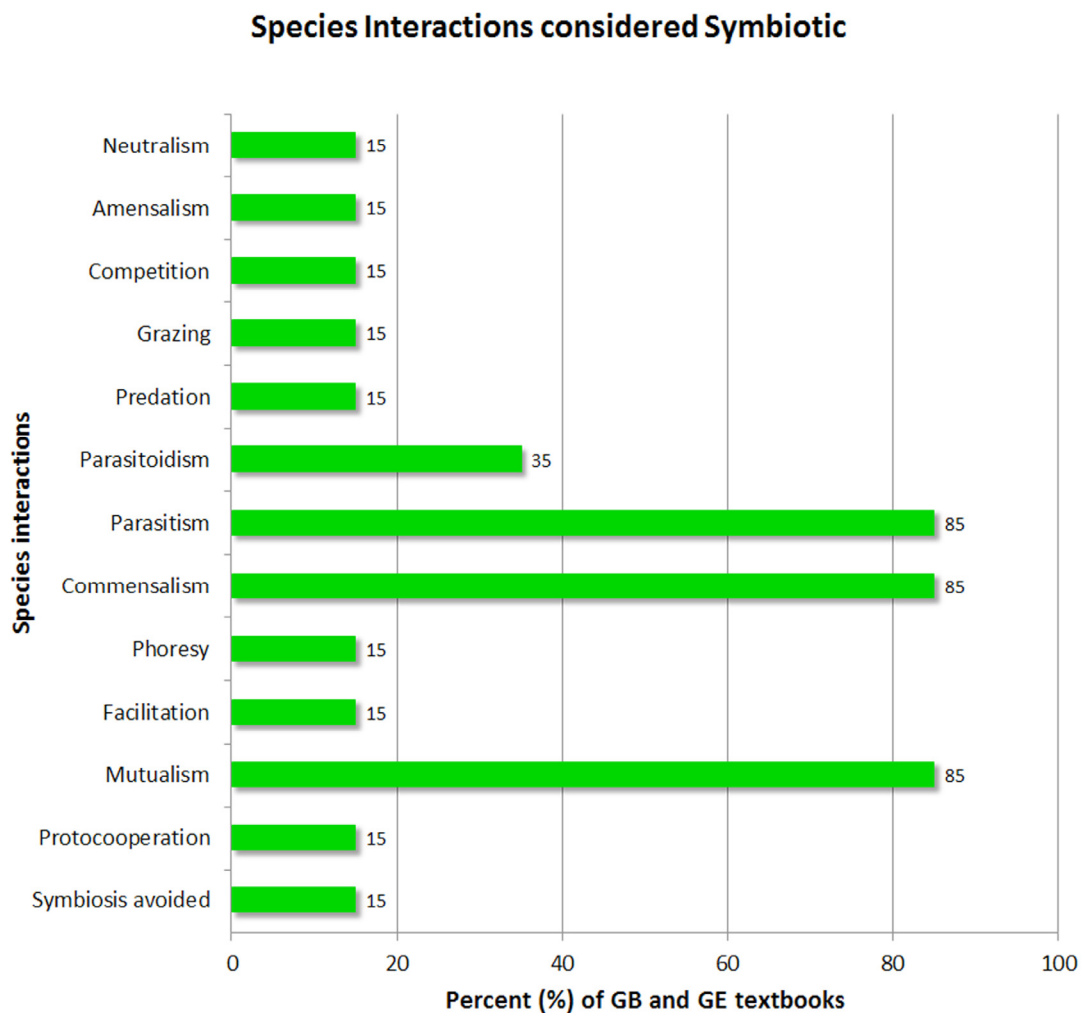


Figure 2. Percent of species interactions considered to be symbiotic by current general biology (GB) and general ecology (GE) textbooks. Three GE textbooks avoided using “symbiosis” entirely, which accounts for mutualism, commensalism, and parasitism reaching only 85%

Considering all species interactions, regardless of symbiosis, 100% of GB and GE textbooks discussed competition, grazing, predation, parasitism, commensalism, and mutualism (Figure 3). Most textbooks discussed parasitoidism (80%), while fewer discussed *amensalism* (30%), *neutralism* (25%), *facilitation* (15%), *protooperation* (10%), and *phoresy* (5%) (Figure 3). Although *amensalism* was discussed in only 30% of GB and GE textbooks, even less (20%) defined it as a form of competition, while 45% of them discussed *allelopathy* by itself (20%) or under *amensalism* (25%). *Facilitation* was used by 45% of GB and GE textbooks in relation to ecological succession, but only 15% used it as a +/0 or +/+ species interactions (Krebs, 2009; Reece et al., 2011; Solomon et al., 2011). Also, *detritivory* (Figure 3) was described in three GE textbooks (30%) as a type of commensalism (+/0), where one species benefits (the detritivore), while the other species is neutrally affected because it is dead (Krohne, 2001; Begon et al., 2006; Ricklefs, 2008).

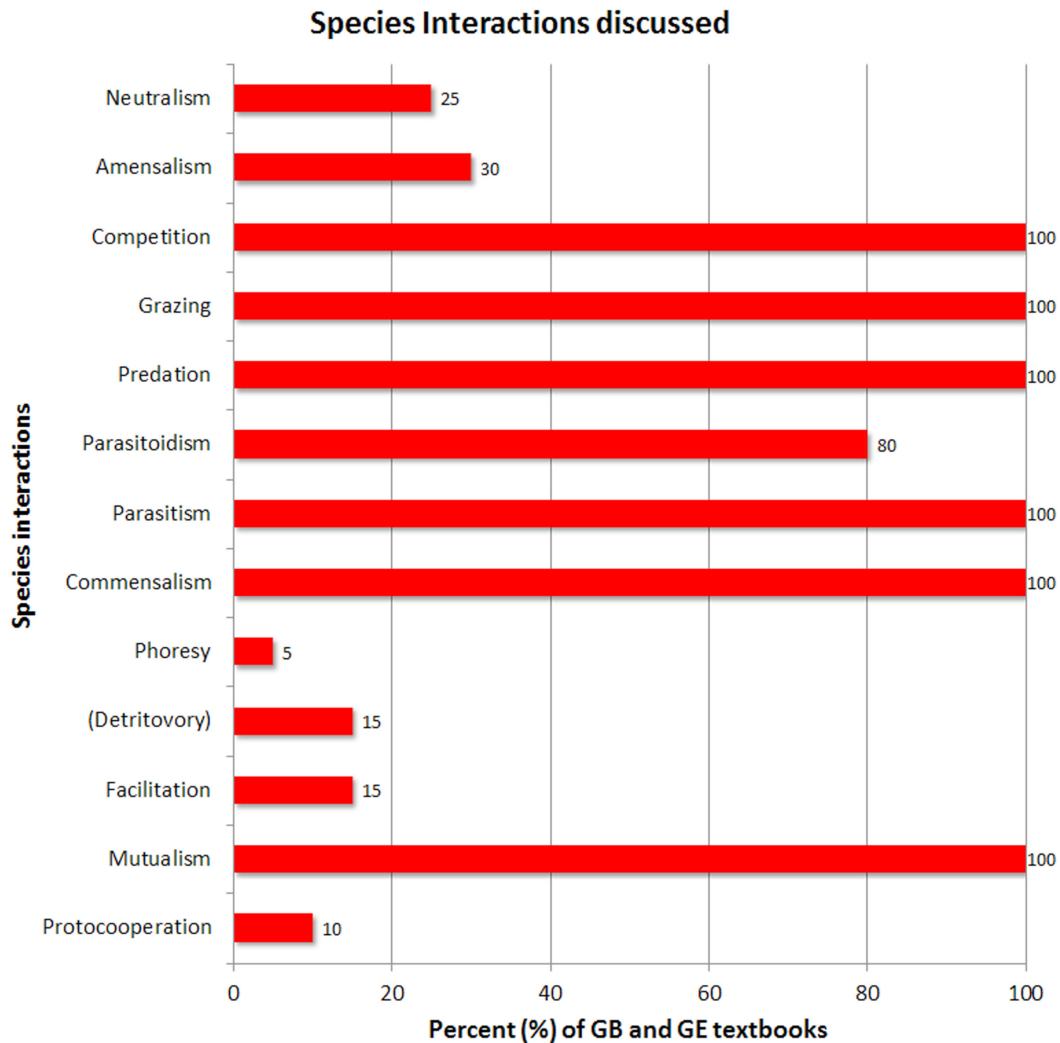


Figure 3. Percent of various species interactions discussed by current general biology (GB) and general ecology (GE) textbooks, regardless of symbiosis. (Detritovory) is in parentheses due to some textbooks considering it a species interaction, although one species is dead

Three textbooks viewed *antagonism* or *exploitation* (not shown in graphs) to be umbrella terms that include various +/- species interactions. Sadava et al. (2011) included parasitism, predation, and herbivory under antagonism, while Molles (2010) included parasitism, predation, herbivory, and disease, and Sharma (2009) included parasitism, predation, and grazing under exploitation.

3.1 Intimacy and Constancy

In relation to criteria that constitute a symbiosis, “intimacy” and/or “constancy” in the species interaction are often discussed as being required. The highest proportion (45%) of GB and GE textbooks considered “intimacy” alone to be required in a symbiosis, while 25% required “intimacy and constancy” (Figure 4). Another 15% considered symbiosis to be “intimate/constant” or “loose/temporary” and 15% did not discuss “intimacy or constancy” (Figure 4).

Intimacy and Constancy in Symbiosis

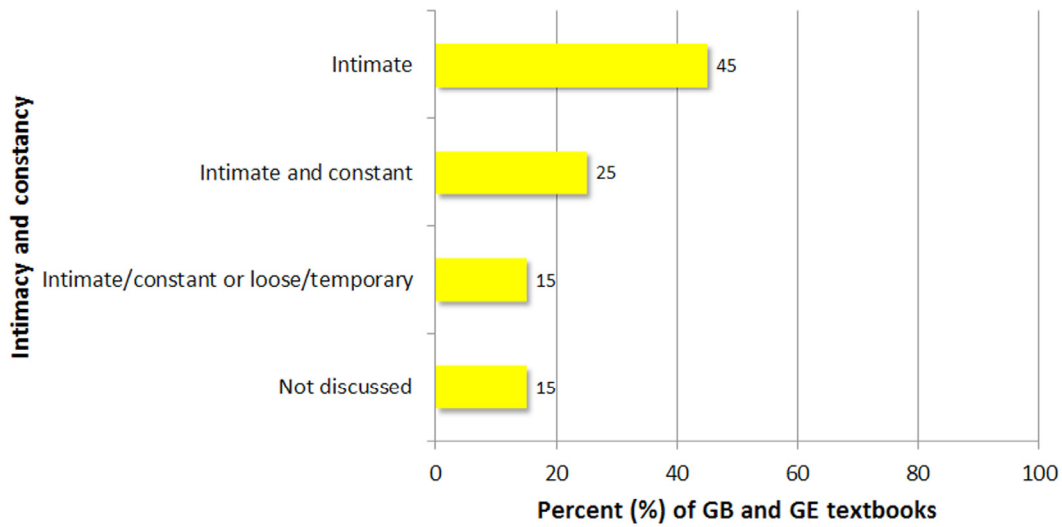


Figure 4. Percent of current general biology (GB) and general ecology (GE) textbooks that require “intimacy” and “constancy” for a symbiosis

3.2 Ecto-/Endosymbiotic Usage

Only 5% of GB and GE textbooks used *ecto-/endosymbiosis* (Figure 5) and this represents only one GE textbook (Odum & Barrett, 2005) using these terms in relation to extant species interactions. Although all GB textbooks used endosymbiosis in relation to endosymbiotic theory (Margulis, 1967), only 30% of these used it in relation to species interactions occurring today as well. None of the GE textbooks discussed endosymbiotic theory. Smith and Smith (2009) used *nonsymbiotic* as a synonym for ectosymbiosis. *Ecto-/endoparasitism* were used in 55% of GB and GE textbooks, while *ecto-/endocommensalism* and *ecto-/endomutualism* were not used at all (Figure 5). For additional usage of ecto-/endo-, 40% of GB and GE textbooks used *ecto-/endomycorrhizae* (Figure 5).

Usage of Ecto-/Endosymbiosis

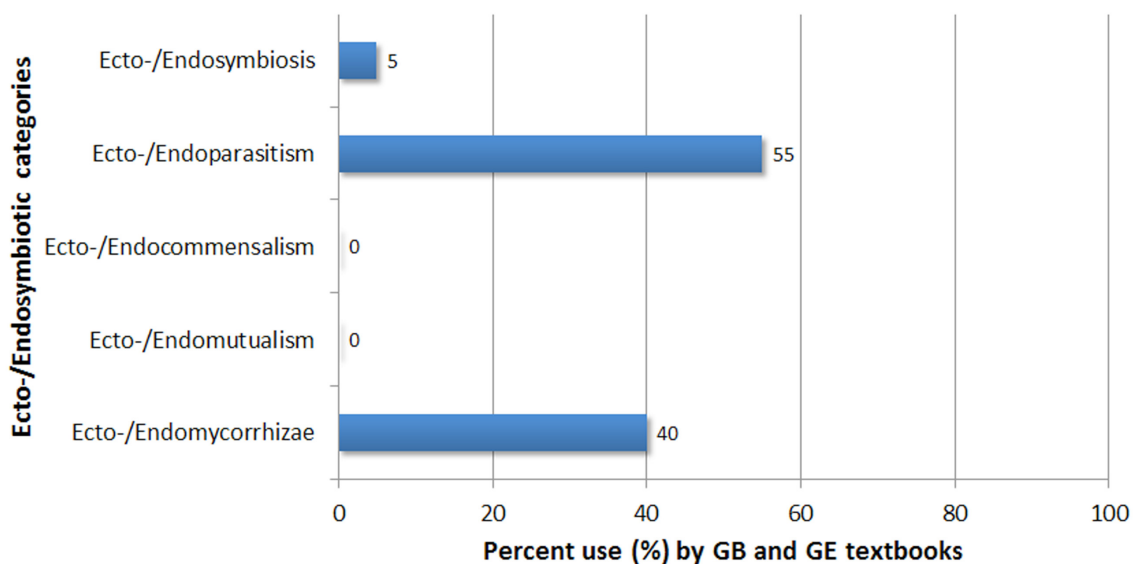


Figure 5. Percent use of ectosymbiosis and endosymbiosis, and related ecto-/endo- terminology, by current general biology (GB) and general ecology (GE) textbooks

3.3 Symbiont versus Symbiote

Symbiote usage was nonexistent (0%) in GB and GE textbooks, with *symbiont* being used in only 55% of these textbooks. As a subset, “host with symbiont” was used in 25% of GB and GE textbooks, rather than just two symbionts.

3.4 Predation, Parasitism, Carnivory, and Herbivory

In predation usage, *predator* and *prey* were both defined as organisms in 90% of GB and GE textbooks, versus 10% as animals only (Figure 6). Predation and parasitism were viewed as being very similar in 65% of GB and GE textbooks, while 35% viewed parasitism as a type of predation. Parasitoidism was defined as a type of parasitism (30%), predation (15%), and predation and parasitism (15%) in GB and GE textbooks. Discussion of a *pathogen* as a type of parasite was found in 40% of GB and GE textbooks.

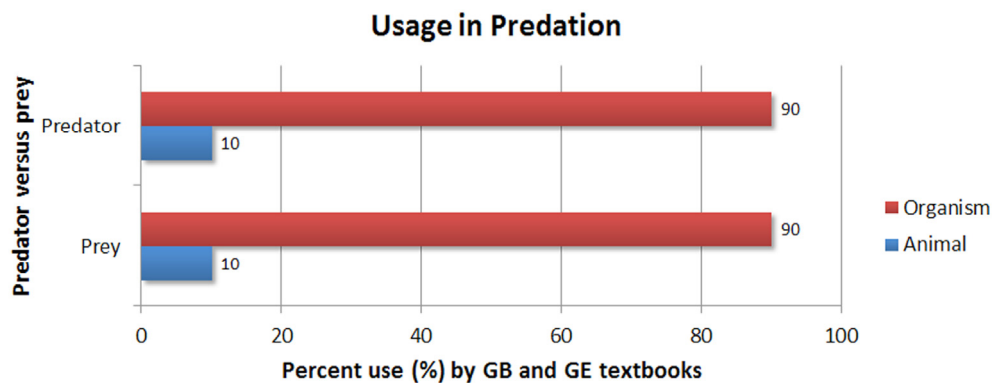


Figure 6. Percent use of *organism* or *animal* in defining predator and prey in predation by current general biology (GB) and general ecology (GE) textbooks

In carnivory usage, a *carnivore* was defined as an organism in 55% of GB and GE textbooks, versus 45% as an animal only (Figure 7). In herbivory usage, an *herbivore* was defined as an organism in 75% of GB and GE textbooks, versus 25% as an animal only (Figure 7). Also, herbivory was viewed as being very similar to predation and parasitism in only 15% of GB and GE textbooks. For the four feeding modes of +/- species interactions, 25% of GB and GE textbooks attempted an integrative presentation to predation, parasitism, parasitoidism, and grazing/herbivory and 40% to predation, parasitism, and grazing/herbivory (no parasitoidism), while 35% did not discuss these interactions together (Figure 8). Only one GB or GE textbook (5%) integrated the concepts of intimacy and lethality (Stiling, 1999) in relation to predation, parasitism, parasitoidism, and grazing/herbivory (Brooker et al., 2011).

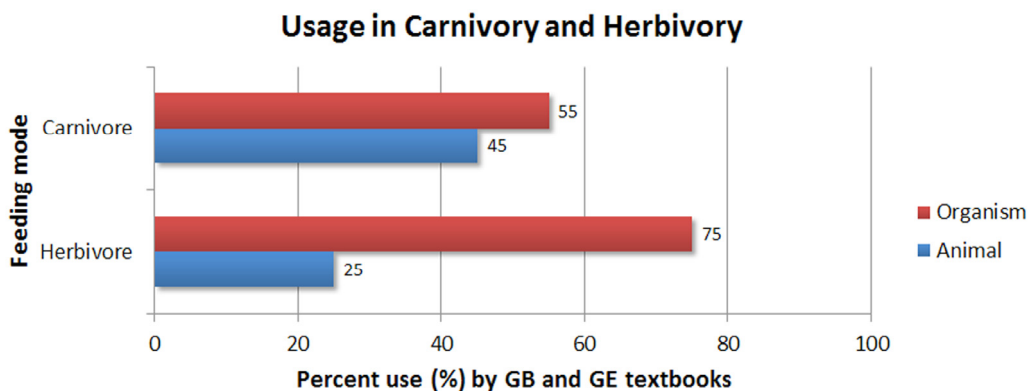


Figure 7. Percent use of *organism* or *animal* in defining carnivore and herbivore by current general biology (GB) and general ecology (GE) textbooks

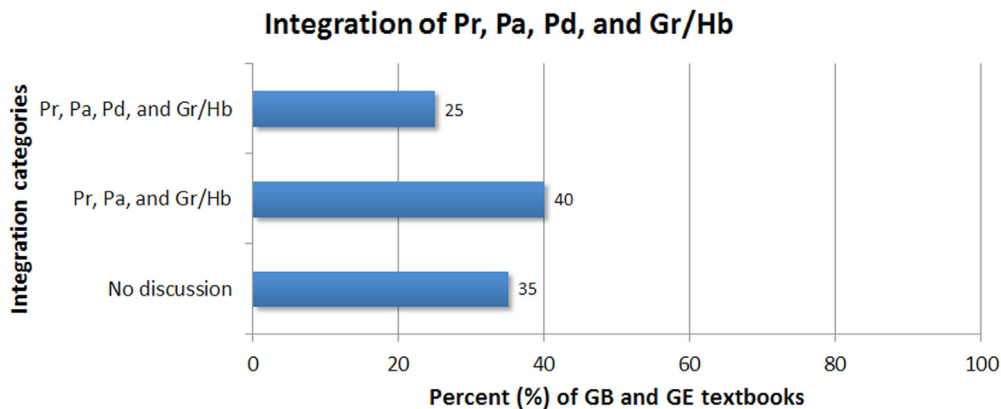


Figure 8. Percent of current general biology (GB) and general ecology (GE) textbooks that attempt to integrate relationships of predation (Pr), parasitism (Pa), parasitoidism (Pd), and grazing (Gr)/herbivory (Hb)

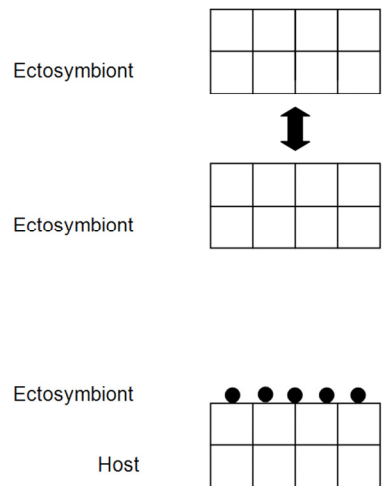
4. Discussion

This review clearly demonstrates that all entry-level biology (i.e. GB) textbooks have returned to de Bary's definition of symbiosis. Usage of the restrictive definition has essentially disappeared in GB and GE textbooks. It is recognized in only four GE textbooks (3 in glossary only), all of which promote broader definitions while covering symbiosis in textbook chapters (Bush, 2003; Odum & Barrett, 2005; Krebs, 2009; Sharma, 2009). General ecology textbooks also exhibited a higher diversity of broad definitions than GB textbooks, as well as avoiding the usage of symbiosis (Krohne, 2001; Molles, 2010; Miller & Spoolman, 2012). This avoidance was probably due to the historical confusion as to what constitutes a symbiosis. Also, very broad definitions (i.e. all species interactions) were used by three of the GE textbooks (Odum & Barrett, 2005; Krebs, 2009; Sharma, 2009) (Figure 2). These textbook authors agree with the ideas of McDougall (1918), Starr (1975), Lewis (1985), and Peacock (2011) that any interaction between two species is a symbiosis.

When combining "intimate" and "intimate/constant," 70% of GB and GE textbooks considered intimacy as a requirement for a symbiosis. Conversely, 30% did not feel "intimacy" or "constancy" is required or important enough to discuss or define. De Bary himself discussed looser species interactions as being symbiotic (McDougall, 1918; Hegner, 1929; Read, 1970; Whitfield, 1979; Lewis, 1985; Sapp, 1994; Paracer & Ahmadjian, 2000).

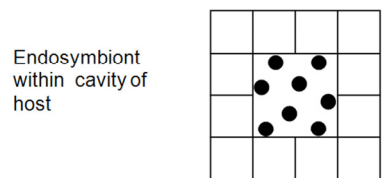
Use of ecto- and endosymbiosis appears to have been proposed by Caullery (1952), followed by endorsement from Starr (1975), Smith and Douglas (1987), and Peacock (2011). Logically, these terms should be used, when considering the common usage of ecto-/endoparasitism and ecto-/endomycorrhizae in textbooks (Figure 5). Although 55% of the textbooks in this study used endosymbiosis, a majority (50%) used it in relation to endosymbiotic theory and of those only 15% additionally included the usage in relation to current species interaction. Only one GE textbook (5%) discussed ectosymbiosis in contrast to endosymbiosis (Odum & Barrett, 2005). Several authors stress the need for biologists to discern symbioses as either ecto- or endosymbiotic (Smith & Douglas, 1987; Nardon & Charles, 2004; Peacock, 2011) (Figure 9). When applying such a scheme, endosymbiosis can only occur in mutualism, commensalism, parasitism, and parasitoidism, while all species interactions can be ectosymbiotic (Figure 10).

Ectosymbiosis

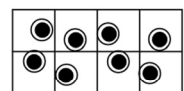


Endosymbiosis

Extracellular

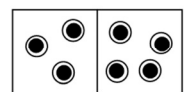


Endosymbiont between cells in host tissue (intercellular)



Intracellular

Endosymbiont within membrane-bound vacuoles



One membrane separates host and endosymbiont

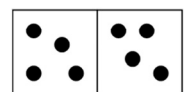


Figure 9. Various types of ectosymbiosis and endosymbiosis (Modified from Smith & Douglas, 1987)

Squares represent cells of multicellular host organisms. Black dots represent smaller endosymbionts or ectosymbionts. Complete circles surrounding endosymbionts (black dots) represent membrane-bound vacuoles that contain these endosymbionts. Circles surrounding endosymbionts (black dots) that touch a cell line (i.e. cell membrane) are technically extracellular, because they are essentially trapped in the invaginations of the host cell membranes between adjacent cells. Endosymbionts entirely surrounded by host cells represent an extracellular endosymbiosis in the body cavity of a host (e.g. protozoans in a gastrointestinal tract). The bottom diagram of ectosymbiosis illustrates more intimate associations of ectomutualism, ectocommensalism, ectoparasitism, and ectoparasitoidism. The top diagram of ectosymbiosis represents less intimate associations of ectomutualism, ectocommensalism, ectoparasitism, and ectoparasitoidism, as well as predation, grazing, amensalism, antagonism, and neutralism. Although ectosymbiosis can be subdivided into two subtypes, we prefer not to use *exosymbiosis* (Peacock, 2011) for less intimate associations (top diagram) due to its synonymous connotation.

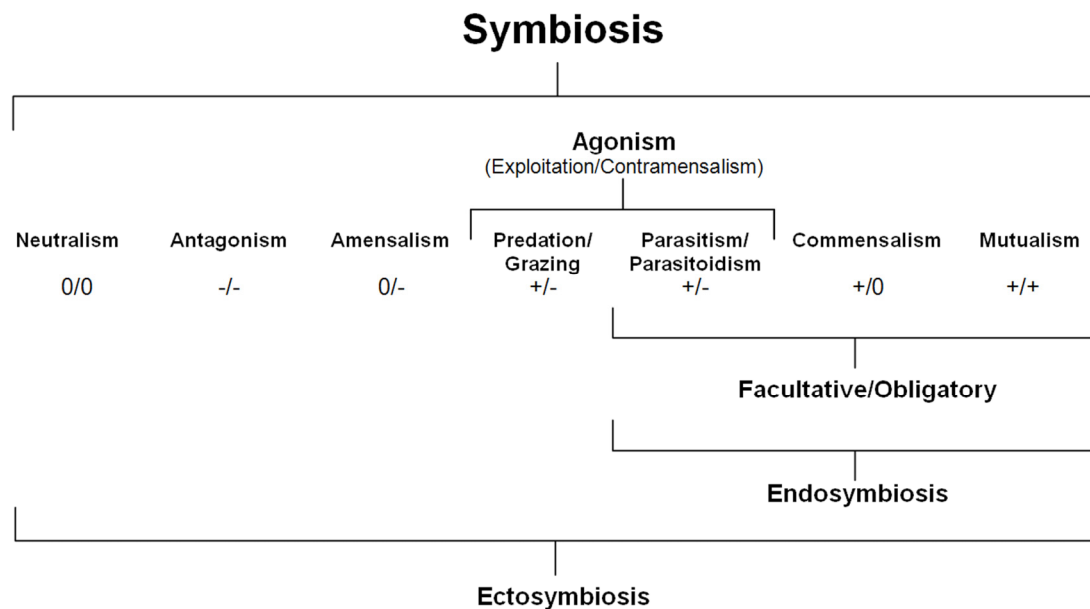


Figure 10. Simplified and inclusive scheme of symbiosis

For any particular pair of interacting species: + = beneficial effect, - = harmful effect, and 0 = neutral effect. This scheme recognizes that endosymbiosis can be subdivided into intracellular/extracellular (Figure 9) and that ectosymbiosis can be subdivided into two subtypes, but we prefer not to use *exosymbiosis* (Peacock, 2011) due to its synonymous connotation.

Increased use of ecto-/endomutualism and ecto-/endocommensalism would also clarify the degree of intimacy and constancy. These terms are occasionally used in the primary literature, but none were found in the GB and GE textbooks used in this study.

Abrams (1987) states that problems exist for two (-/- and +/-) of the six Odum-type classification names (Figure 10), because competition and predation have mechanistic connotations, and require new names, which he did not propose. Clarke (1954) introduced the umbrella term *antagonism*, which included any negative species interactions [i.e. *exploitation* (+/-), *antibiosis* (-/0), and *competition* (-/-)]. Antagonism was adopted by Lewis (1985), but he also used *agonism* for +/- interactions, instead of exploitation, and we concur with this usage (Figure 10). Older terms such as *inquilinism* or *allotrophy* (+/0), *antibiosis* or *allolimy* (-/0), and *synnecrosis* (-/-) (Burkholder, 1952; Caullery, 1952; Clarke, 1954) and newer terms like *agonism*, *enslavement*, and *contramensalism* (+/-) (Lewis, 1985; Gould & Keeton, 1996; Hodge & Arthur, 1996) have essentially been avoided by other authors, which explains their absence in the textbooks of this study. Reece et al. (2011) defined facilitation as when “species can have positive effects (+/+ or 0/+) on the survival and reproduction of other species without necessarily living in direct and intimate contact of a symbiosis.” *Indirect effects* are important in the understanding of species interactions and symbiosis (Abrams, 1987; Wooten, 1994), but were briefly discussed in only 20% of GB and 50% of GE textbooks.

Nardon and Charles (2004) continue to argue that symbiote is historically and epistemologically correct, not symbiont, as also stated by others (Meyer, 1925; Cleveland, 1926; Hertig et al., 1937; Read, 1970; Starr, 1975). However, symbiont appears to be the accepted term used by all of the GB and GE textbooks in this study, because none use symbiote.

Since all GB and GE textbooks described parasitism as similar to (or a type of) predation, this implies that predation can be symbiotic. Also, the separation is blurry when considering that parasites sometimes kill their hosts. There was a consensus in GB and GE textbooks to use organism, rather than animal, for describing predators and prey. This is very appropriate due to the predatory nature of carnivorous plants (e.g. bladderworts, sundews, Venus flytraps, pitcher plants, and butterworts), as well as frugivores and granivores are predatory animals that often kill plant embryos in seeds. However, there is more confusion in the usage of carnivory and herbivory. Clarity could be facilitated by the use of *zoo-* and *phyto-* prefaces to discern when the

carnivore/herbivore is an animal-like or plant-like organism. We propose using *zoocarnivory* and *zooherbivory*, when the carnivore/herbivore is an animal or animal-like organism (e.g. wolves preying on caribou versus bison grazing on grass). Conversely, use *phytocarnivory* and *phytoherbivory* when the carnivore/herbivore is a plant or plant-like organism (e.g. carnivorous plants versus parasitic plants).

Grazing and *herbivory* are usually used interchangeably in GB and GE textbooks. It often evokes images of ungulates foraging on grass or woody vegetation, but grazing can also be on animals. Stiling (1999) proposed that grazing is a mode of feeding and is not synonymous with herbivory. He contrasts four types of +/- species interactions that we propose are *agonistic*: Predation, grazing, parasitism, and parasitoidism by relating them to *intimacy* and *lethality* (Figure 11). There are four possible combinations: Predation has low intimacy and high lethality, parasitism has high intimacy and low lethality, parasitoidism has high intimacy and lethality, and grazing has low intimacy and lethality. Only one GB and GE textbook presented this concept, because Stiling (1999) is a coauthor (Brooker et al., 2011). Unfortunately, Stiling replaced grazing with herbivory, a less accurate term (Brooker et al., 2011). This unifying, agonistic concept is important to present in all entry-level biology and ecology textbooks, because predators, prey, parasites, and hosts can also be plants, while some grazers are often insects on plants (e.g. grasshoppers, leafhoppers, mosquitoes, etc.) or animals on animals (e.g. lampreys, vampire bats, fleas, bed bugs, etc.).

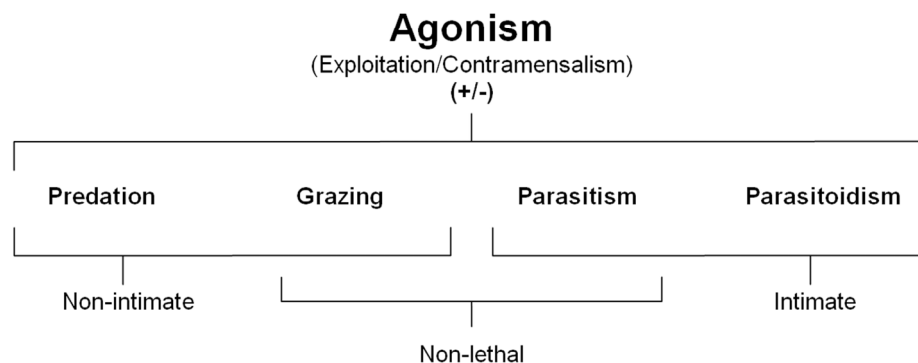


Figure 11. Agonistic (+/-) species interactions showing the differences in intimacy and lethality (Stiling, 1999)

5. Conclusion

Considering the turbulent history of symbiosis (Martin & Schwab, 2012), this much-needed review has presented the variation in symbiotic terminology quantitatively to more objectively understand the current trends in usage. The complexity of symbiotic phenomena, the prolonged history of confusion, and the various attempts to unify the field have all warranted a thorough presentation and evaluation at this time. It may be necessary to periodically publish reports, such as this one, to quantify trends and the current state of understanding in symbiotic terminology. This may be one solution to reducing confusion, which will invariably unify and stabilize term usage. As demonstrated in this paper, times are different today in our understanding of symbiotic phenomena and there is resurgent interest with new perspectives in the field. The emerging changes do indicate that the restrictive definition has all but disappeared and biologists who avoid the term can now use at least de Bary's definition without criticism. Should most or all biologists embrace *symbiosis* due to consensus and resolution of the prolonged confusion, it will liberate this beautiful term that simply means "living together."

Acknowledgements

The authors would like to thank Arthur Kroetz for producing the final figures in this paper. Thanks goes to students in the 2002 *Symbiosis* (Biol 370) course at California State University San Bernardino for their ideas. Special thanks goes to the Biology Department at La Sierra University for allowing Bradford Martin a sabbatical during autumn 1999 to initiate research on this topic. Lastly, we are grateful to the publishers at Benjamin/Cummings, Blackwell, Brooks/Cole, McGraw-Hill, Pearson, Pearson Benjamin Cummings, Prentice-Hall, Sinauer Associates, and W. H. Freeman for providing current editions of general biology and/or ecology textbooks.

References

- Abrams, P. A. (1987). On classifying interactions between populations. *Oecologia*, *73*, 272-281. <http://dx.doi.org/10.1007/BF00377518>
- Ahmadjian, V., & Paracer, S. (1986). *Symbiosis: An introduction to biological associations* (1st ed.). Hanover, NH: University Press of New England.
- Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: From individuals to ecosystems* (4th ed.). Malden, MA: Blackwell Publishing.
- Bronstein, J. L. (1994). Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution*, *9*, 214-217. [http://dx.doi.org/10.1016/0169-5347\(94\)90246-1](http://dx.doi.org/10.1016/0169-5347(94)90246-1)
- Brooker, R. J., Widmaier, E. P., Graham, L. E., & Stiling, P. D. (2011). *Biology* (2nd ed.). New York, NY: McGraw-Hill.
- Burkholder, P. R. (1952). Cooperation and conflict among primitive organisms. *American Scientist*, *40*, 601-631.
- Bush, M. B. (2003). *Ecology of a changing planet* (3rd ed.). Upper Saddle River, NJ: Prentice-Hall, Inc.
- Caullery, M. (1952). *Parasitism and symbiosis*. London, UK: Sidgwick and Jackson Limited. PMID: 13020016.
- Clarke, G. L. (1954). *Elements of ecology*. New York, NY: John Wiley & Sons.
- Cleveland, L. R. (1926). Symbiosis among animals with special reference to termites and their intestinal flagellates. *Quarterly Review of Biology*, *1*, 51-59. <http://dx.doi.org/10.1086/394236>
- Cooke, R. (1977). *The biology of symbiotic fungi*. London, UK: John Wiley & Sons.
- De Bary, A. (1879). *Die erscheinung der symbiose*. Strassburg, Germany: Verlag von Karl J. Trubner.
- Douglas, A. E. (1994). *Symbiotic interactions*. Oxford, UK: Oxford University Press.
- Douglas, A. E., & Smith, D. C. (1989). Are endosymbioses mutualistic? *Trends in Ecology and Evolution*, *4*, 350-352. [http://dx.doi.org/10.1016/0169-5347\(89\)90090-6](http://dx.doi.org/10.1016/0169-5347(89)90090-6)
- Freeman, S. (2011). *Biological science* (4th ed.). San Francisco, CA: Pearson Benjamin Cummings.
- Gould, J. L., & Keeton, W. T. (1996). *Biological science* (6th ed.). New York, NY: W. W. Norton & Company.
- Guttman, B. S. (1999). *Biology*. Boston, MA: WCB/McGraw-Hill. PMID: 144313.
- Hegner, R. (1929). Introduction. In R. Hegner, F. M. Root, & D. L. Augustine (Eds.), *Animal parasitology* (pp. 3-22). New York, NY: D. Appleton-Century Company.
- Hertig, M., Taliaferro, W. H., & Schwartz, B. (1937). Supplement to the report of the twelfth annual meeting of the American Society of Parasitologists: Report of the committee on terminology. *Journal of Parasitology*, *23*, 325-329.
- Hodge, S., & Arthur, W. (1996). Contramensalism interactions between species. *Oikos*, *77*, 371-375. <http://dx.doi.org/10.2307/3546080>
- Kormondy, E. J. (1996). *Concepts of ecology*. Upper Saddle River, NJ: Prentice Hall.
- Krebs, C. J. (2009). *Ecology: The experimental analysis of distribution and abundance* (6th ed.). San Francisco, CA: Pearson Benjamin Cummings.
- Krohne, D. T. (2001). *General ecology* (2nd ed.). Pacific Grove, CA: Brooks/Cole.
- Lewin, R. A. (1982). Symbiosis and parasitism-Definitions and evaluations. *Bioscience*, *32*, 254-259. <http://dx.doi.org/10.2307/1308530>
- Lewis, D. H. (1985). Symbiosis and mutualism: crisp concepts and soggy semantics. In D. H. Boucher (Ed.), *The biology of mutualism: Ecology and evolution* (pp. 29-39). Oxford, UK: Oxford University Press. PMID: 4008455.
- Mader, S. S. (2010). *Biology* (10th ed.). New York, NY: McGraw-Hill.
- Margulis, L. (1967). On the origin of mitosing cells. *Journal of Theoretical Biology*, *14*, 255-274.
- Margulis, L. (1990). Words as battle cries-symbiogenesis and the new field of endocytobiology. *Bioscience*, *40*, 673-677. <http://dx.doi.org/10.2307/1311435>
- Martin, B. D., & Schwab, E. (2012). Symbiosis: "Living together" in chaos. *Studies in the History of Biology*, *4*(4), 7-25.

- McDougall, W. B. (1918). The classification of symbiotic phenomena. *Plant World*, 21, 250-256.
- Meyer, K. F. (1925). The "bacterial symbiosis" in the concretion deposits of certain operculate land mollusks of the families Cyclostomatidae and Annulariidae. *Journal of Infectious Diseases*, 36, 1-99. <http://dx.doi.org/10.1093/infdis/36.1.1>
- Miller, G. T., & Spoolman, S. E. (2012). *Essentials of ecology* (6th ed.). Belmont, CA: Brooks/Cole.
- Miller, K. R., & Levine, J. S. (2010). *Biology* (1st ed.). Boston, MA: Pearson.
- Molles, M. C., Jr. (2010). *Ecology: Concepts and applications* (5th ed.). New York, NY: McGraw-Hill.
- Moran, N. A. (2006). Symbiosis. *Current Biology*, 16, 866-871. <http://dx.doi.org/10.1016/j.cub.2006.09.019>
- Nardon, P., & Charles, H. (2004). Morphological aspects of symbiosis. In J. Seckbach (Ed.), *Symbiosis: Mechanisms and model systems* (pp. 13-14). New York, NY: Kluwer Academic Publishers.
- Odum, E. P. (1971). *Fundamentals of ecology* (3rd ed.). Philadelphia, PA: Saunders College Publishing.
- Odum, E. P., & Barrett, G. W. (2005). *Fundamentals of ecology* (5th ed.). Belmont, CA: Thomson Brooks/Cole.
- Paracer, S., & Ahmadjian, V. (2000). *Symbiosis: An introduction to biological associations* (2nd ed.). New York, NY: Oxford University Press.
- Peacock, K. A. (2011). Symbiosis in ecology and evolution. In D. M. Gabbay, P. Thagard, & J. Woods (Eds.), *Handbook of the philosophy of science: Philosophy of ecology* (pp. 219-250). San Diego, CA: North Holland. <http://dx.doi.org/10.1016/B978-0-444-51673-2.50009-1>
- Pianka, E. R. (2000). *Evolutionary ecology* (6th ed.). San Francisco, CA: Benjamin/Cummings.
- Pound, R. (1893). Symbiosis and mutualism. *American Naturalist*, 27, 509-520. <http://dx.doi.org/10.1086/275742>
- Raven, P. H., Johnson, G. B., Mason, K. A., Losos, J. B., & Singer, S. R. (2011). *Biology* (9th ed.). New York, NY: McGraw-Hill.
- Read, C. P. (1970). *Parasitism and symbiology*. New York, NY: Ronald Press Company.
- Reece, J. B., Urry, L. A., Cain, M. L., Wasserman, S. A., Minorsky, P. V., & Jackson, R. B. (2011). *Campbell: Biology* (9th ed.). San Francisco, CA: Pearson Benjamin Cummings.
- Richardson, J. L. (1977). *Dimensions of ecology*. Baltimore, MD: Williams & Wilkins Company.
- Ricklefs, R. E. (2008). *The economy of nature* (6th ed.). New York, NY: W. H. Freeman and Company.
- Russell, P. J., Hertz, P. E., & McMillan, B. (2011). *Biology: The dynamic science* (2nd ed.). Belmont, CA: Brooks/Cole.
- Sadava, D., Hillis, D. M., Heller, H. C., & Berenbaum, M. (2011). *Life: The science of biology* (9th ed.). Sunderland, MA: Sinauer Associates, Inc.
- Saffo, M. B. (1992). Coming to terms with a field: Words and concepts in symbiosis. *Symbiosis*, 14, 17-31.
- Sapp, J. (1994). *Evolution by association: A history of symbiosis*. New York, NY: Oxford University Press.
- Sapp, J. (2004). The dynamics of symbiosis: An historical overview. *Canadian Journal of Botany*, 82, 1046-1056. <http://dx.doi.org/10.1139/b04-055>
- Scott, G. D. (1969). *Plant symbiosis*. New York, NY: St. Martin's Press.
- Sharma, P. D. (2009). *Ecology and environment* (10th ed.). New Delhi, India: Rastogi Publications.
- Smith, D. C., & Douglas, A. E. (1987). *The biology of symbiosis*. Baltimore, MD: Edward Arnold.
- Smith, R. L. (1992). *Elements of ecology* (3rd ed.). New York, NY: Harper Collins Publishers.
- Smith, T. M., & Smith, R. L. (2009). *Elements of ecology* (7th ed.). San Francisco, CA: Pearson Benjamin Cummings.
- Solomon, E. P., Berg, L. R., & Martin, D. W. (2011). *Biology* (9th ed.). Belmont, CA: Brooks/Cole.
- Starr, C., & Taggart, R. (1992). *Biology: The unity and diversity of life* (6th ed.). Belmont, CA: Wadsworth Publishing Co.
- Starr, C., & Taggart, R. (1998). *Biology: The unity and diversity of life* (8th ed.). Belmont, CA: Wadsworth Publishing Co.

- Starr, C., Taggart, R., Evers, C., & Starr, L. (2009). *Biology: The unity and diversity of life* (12th ed.). Belmont, CA: Brooks/Cole.
- Starr, M. P. (1975). A generalized scheme for classifying organismic associations in Symbiosis. *Symposia of the Society for Experimental Biology*, 29, 1-20. PMID: 785657.
- Stiling, P. (1999). *Ecology: Theories and applications*. Upper Saddle River, NJ: Prentice Hall, Inc. PMID: 11543430.
- Stock, S. P., Bordenstein, S. R., Odden, J., Oldenburg, D., Reznikoff, W., Werren, J. H., & Selosse, M. A. (2010). Symbiosis instruction: Considerations from the education workshop at the 6th ISS Congress. *Symbiosis*, 51, 67-73. <http://dx.doi.org/10.1007/s13199-010-0077-z>
- Trager, W. (1986). *Living together: The biology of parasitism*. New York, NY: Plenum Press. <http://dx.doi.org/10.1007/978-1-4615-9465-9>
- Whitfield, P. J. (1979). *The biology of parasitism: An introduction to the study of associating organisms*. Baltimore, MD: University Park Press.
- Wilkinson, D. M. (2001). At cross purposes. *Nature*, 412, 485. <http://dx.doi.org/10.1038/35087676>
- Wooten, J. T. (1994). The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, 25, 443-466. <http://dx.doi.org/10.1146/annurev.es.25.110194.002303>