



教育部高等教育司推荐
国外优秀生命科学教学用书

生态学

(第7版)(影印版)

ECOLOGY

Concepts and Applications

(Seventh Edition)



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Education

Manuel C. Molles Jr.

高等教育出版社



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About the Author

Manuel C. Molles Jr. is an emeritus Professor of Biology at the University of New Mexico, where he has been a member of the faculty and curator in the Museum of Southwestern Biology since 1975 and where he continues to write and conduct ecological research. He received his B.S. from Humboldt State University and his Ph.D. from the Department of Ecology and Evolutionary Biology at the University of Arizona. Seeking to broaden his geographic perspective, he has taught and conducted ecological research in Latin America, the Caribbean, and Europe. He was awarded a Fulbright Research Fellowship to conduct research on river ecology in Portugal and has held visiting professor appointments in the Department of Zoology at the University of Coimbra, Portugal, in the Laboratory of Hydrology at the Polytechnic University of Madrid, Spain, and at the University of Montana's Flathead Lake Biological Station.

Originally trained as a marine ecologist and fisheries biologist, the author has worked mainly on river and riparian ecology at the University of New Mexico. His research has covered a wide range of ecological levels, including behavioral ecology, population biology, community ecology, ecosystem ecology, biogeography of stream insects, and the influence of a large-scale climate system (El Niño) on the dynamics of southwestern river and riparian ecosystems. His current research concerns the influence of climate change and climatic variability on the dynamics of populations and communities along steep gradients of temperature and moisture in the mountains of the Southwest. Throughout his career, Dr. Molles has attempted to combine research, teaching, and service, involving undergraduate as well as graduate students in his ongoing projects. At the University of New Mexico, he has taught a broad range of lower division, upper division, and graduate courses, including Principles of Biology, Evolution and Ecology, Stream Ecology, Limnology and Oceanography, Marine Biology, and Community and Ecosystem Ecology. He has taught courses in Global Change and River Ecology at the University of Coimbra, Portugal, and General Ecology and Groundwater and Riparian Ecology at the Flathead Lake Biological Station. Dr. Manuel Molles was named Teacher of the Year by the University of New Mexico for 1995–1996 and Potter Chair in Plant Ecology in 2000. In 2014, he received the Eugene P. Odum Award from the Ecological Society of America based on his “ability to relate basic ecological principles to human affairs through teaching, outreach and mentoring activities.”



Dedication

To Mary Anne
and
Keena

Preface

This book was written for students taking their first undergraduate course in ecology. I have assumed that students in this one-semester course have some knowledge of basic chemistry and mathematics and have had a course in general biology, which included introductions to physiology, biological diversity, and evolution.

Organization of the Book

An evolutionary perspective forms the foundation of the entire textbook, as it is needed to support understanding of major concepts. The textbook begins with a brief introduction to the nature and history of the discipline of ecology, followed by section I, which includes two chapters on natural history—life on land and life in water and a chapter on population genetics and natural selection. Sections II through VI build a hierarchical perspective through the traditional subdisciplines of ecology: section II concerns adaptations to the environment; section III focuses on population ecology; section IV presents the ecology of interactions; section V summarizes community and ecosystem ecology; and finally, section VI discusses large-scale ecology and includes chapters on landscape, geographic, and global ecology. These topics were first introduced in section I within a natural history context. In summary, the book begins with the natural history of the planet, considers portions of the whole in the middle chapters, and ends with another perspective of the entire planet in the concluding chapter. The features of this textbook were carefully planned to enhance the students' comprehension of the broad discipline of ecology.

Features Designed with the Student in Mind

All chapters are based on a distinctive learning system, featuring the following key components:

Student Learning Outcomes: Educators are being asked increasingly to develop concrete student learning outcomes for courses across the curriculum. In response to this need and to help focus student progress through the content, all sections of each chapter in the seventh edition begin with a list of detailed student learning outcomes.

Introduction: The introduction to each chapter presents the student with the flavor of the subject and important background information. Some introductions include historical events related to the subject; others present an example of an ecological process. All attempt

to engage students and draw them into the discussion that follows.

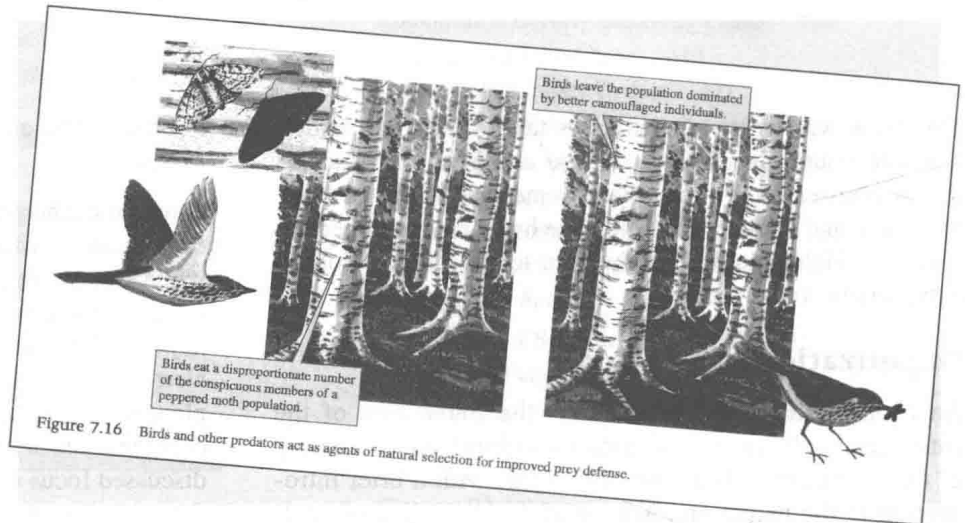
Concepts: The goal of this book is to build a foundation of ecological knowledge around key concepts. I have found that while beginning ecology students can absorb a few central concepts well, they can easily get lost in a sea of details. The key concepts are listed at the beginning of each chapter to alert the student to the major topics to follow and to provide a place where the student can find a list of the important points covered in each chapter. The sections in which concepts are discussed focus on published studies and, wherever possible, the scientists who did the research are introduced. This case-study approach supports the concepts with evidence, and introduces students to the methods and people that have created the discipline of ecology. Each concept discussion ends with a series of concept review questions to help students test their knowledge and to reinforce key points made in the discussion.



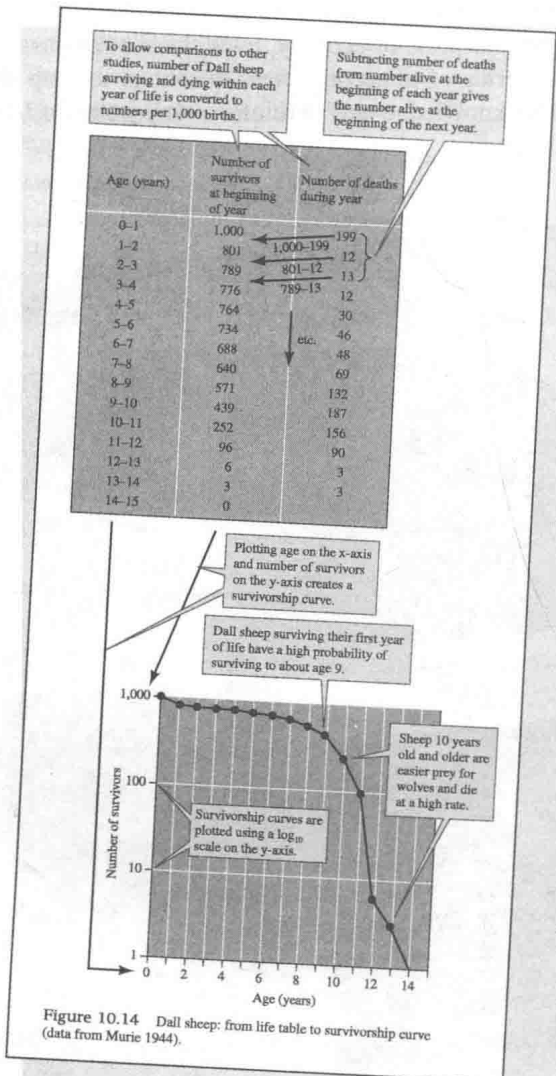
Illustrations: A great deal of effort has been put into the development of illustrations, both photographs and line art. The goal has been to create more effective pedagogical tools through skillful design and use of color, and to rearrange the traditional presentation of information in figures and captions. Much explanatory material is located within the illustrations, providing students with key information where they need it most. The approach also provides an ongoing tutorial on graph interpretation, a skill with which many introductory students need practice.

Detailed Explanations of Mathematics: The mathematical aspects of ecology commonly challenge many students taking their first ecology course. This text carefully explains all mathematical

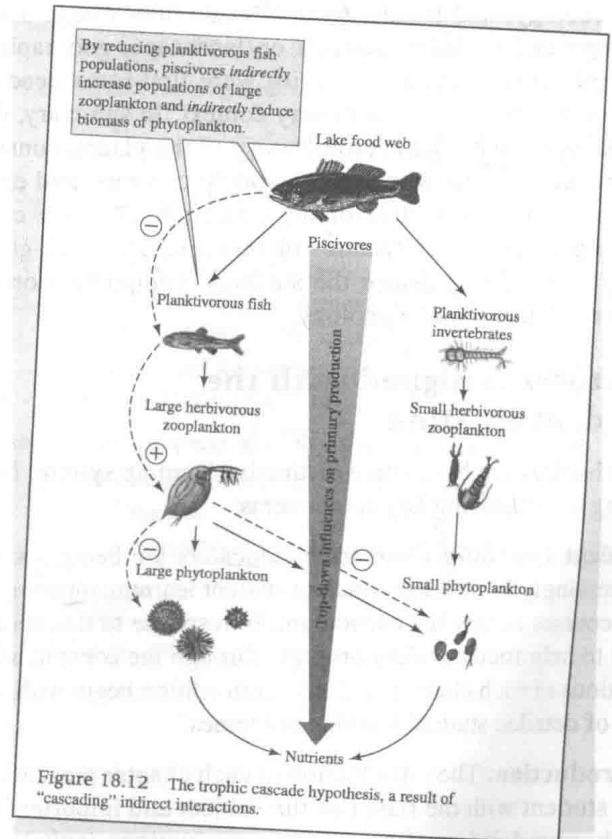
expressions that arise to help students overcome these challenges. In some cases, mathematical expressions are dissected in illustrations designed to complement their presentation in the associated narrative.



Visualizing a process involving a predator and its prey.



Helps students work with and interpret quantitative information, involving converting numerical information into a graph.



Provides a visual representation of a hypothesis involving a set of complex ecological interactions.

“Investigating the Evidence” Boxes: These readings offer “mini-lessons” on the scientific method, emphasizing statistics and study design. They are intended to present a broad outline of the process of science, while also providing step-by-step explanations. The series of boxes begins in chapter 1 with an overview of the scientific method, which establishes a conceptual context for more specific material in the next 21 chapters. The last reading wraps up the series with a discussion of electronic literature searches. Each Evidence box ends with one or more questions, under the heading “Critiquing the Evidence.” This feature is intended to stimulate critical thinking about the box content.

Applications: Many undergraduate students want to know how abstract ideas and general relationships can be applied to the ecological problems we face in the contemporary world. They are concerned with the practical side of ecology and want to know more about how the tools of science can be applied. Including a discussion of applications in each chapter motivates students to learn more of the underlying principles of ecology. In addition, it seems that environmental problems are now so numerous and so pressing that they have erased a once easy distinction between general and applied ecology.

End-of-Chapter Material:

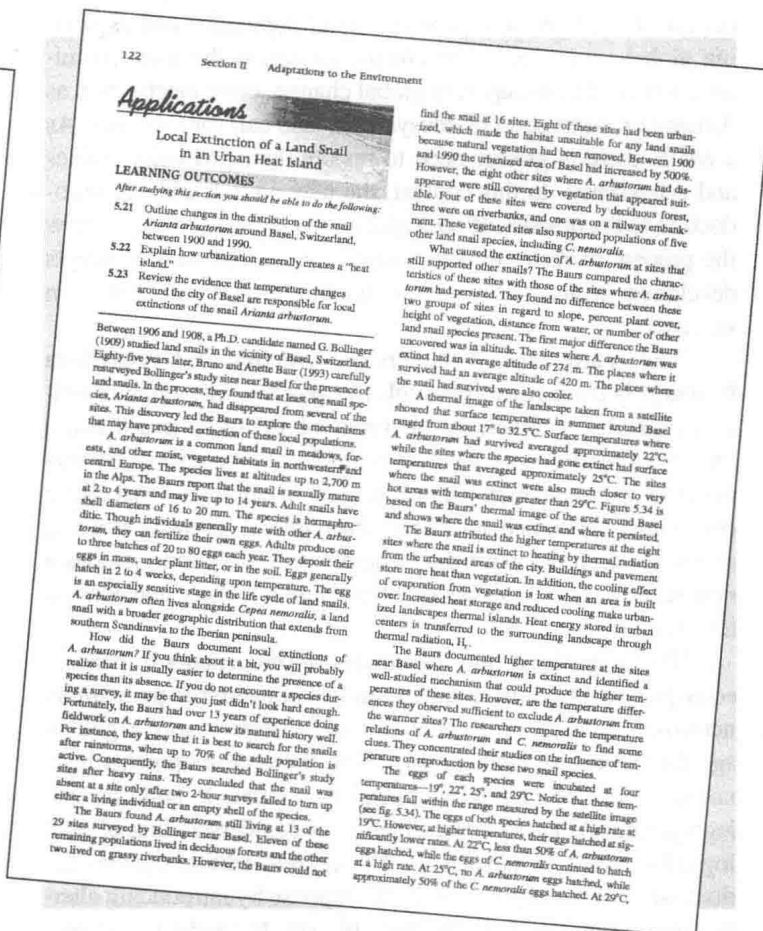
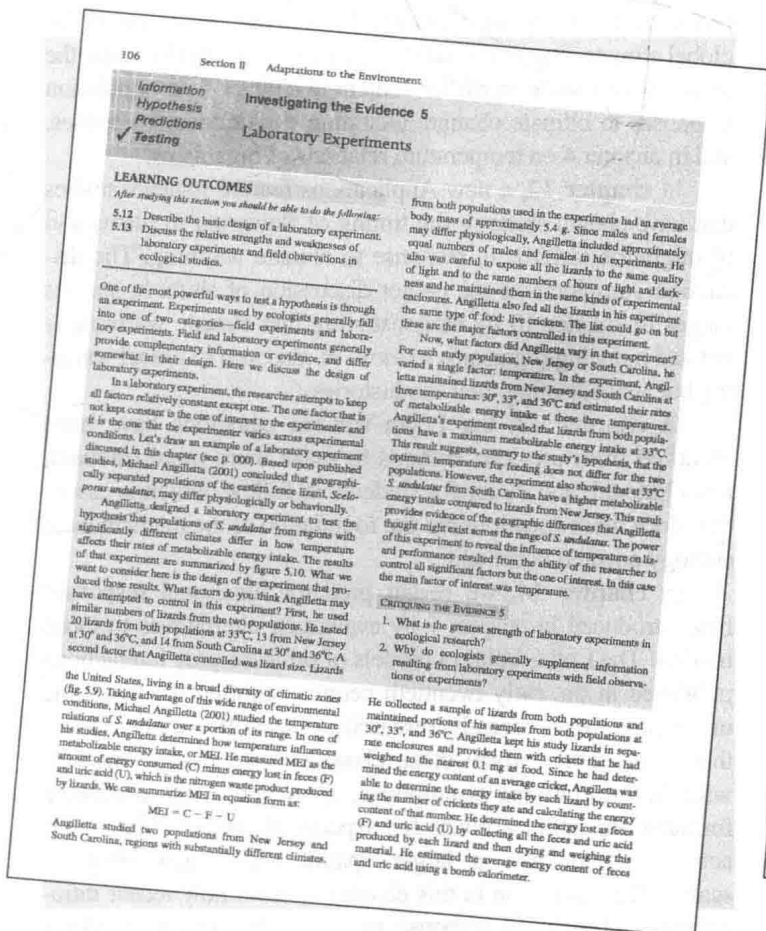
- **Summary** The chapter summary reviews the main points of the content. The concepts around which each

chapter is organized are boldfaced and redefined in the summary to reemphasize the main points of the chapter.

- **Key Terms** The listing of key terms provides page numbers for easy reference in each chapter.
- **Review Questions** The review questions are designed to help students think more deeply about each concept and to reflect on alternative views. They also provide a place to fill in any remaining gaps in the information presented and take students beyond the foundation established in the main body of the chapter.

End-of-Book Material:

- **Appendixes** One appendix, “Statistical Tables,” is available to the student for reference. Answers to Concept Review questions and answers to Critiquing the Evidence are now available with the book’s instructor resources.
- **Glossary** List of all key terms and their definitions.
- **References** References are an important part of any scientific work. However, many undergraduates are distracted by a large number of references within the text. One of the goals of a general ecology course should be to introduce these students to the primary literature without burying them in citations. The number of citations has been reduced to those necessary to support detailed discussions of particular research projects.
- **Index**



New to the Seventh Edition

The seventh edition expands the pedagogy by beginning all sections of every chapter with a list of student learning outcomes—over 450 student learning outcomes in all. These outcomes are largely based on fundamental learning outcomes for material covered in the text:

1. Define key terms.
2. Explain the main concepts.
3. Evaluate the strength of research presented in support of main concepts, including a critique of study design.
4. Interpret statistical evidence bearing on concepts, expressed in graphical and numerical form.
5. Apply the main concepts to interpretation of new situations.

A content thread focused on global change has been developed and distributed across chapters, emphasizing global climate change. Students and instructors increasingly look for ways to connect the concepts and practice of ecological science to environmental issues arising from global climate change. The present edition explores how species are adjusting their distributions and their critical life history events as climate changes. The final chapter ends with a review of projected impacts of climate change on ecosystems and human populations, infrastructure, and economic systems.

This edition also builds on previous discussions of human disturbance of ecosystems to consider how damaged ecosystems can be restored. The extent and intensity of human impact on the biosphere grows with our population and expanding global economy. While climate change is the most prominent aspect of contemporary global change, other facets, such as damage or destruction of ecosystems, also call for solutions. As a result, there is greater need to restore damaged communities and ecosystems. In this context, the new edition adds an introduction to the practice of ecological restoration, focusing on how the process of restoring ecosystems can benefit from concepts developed in academic studies of community and ecosystem succession.

The relationship between biodiversity and ecosystem function is introduced through the positive influence of primary producer diversity on rates of primary production. Studies of biodiversity and ecosystem function are key elements in ecology's foundation. Connecting these elements helps create conceptual coherence across the discipline. A growing body of recent research does just that. Therefore, this edition includes a new section on the connection between biodiversity and ecosystem function.

The seventh edition introduces developments in trophic ecology that build on classical models of predator-prey interactions. The early to middle twentieth century was a golden age for theoretical ecology. However, those developments have not stopped. Contemporary ecologists continue to build on that legacy, improving our representation and understanding of ecological systems as they do so. The seventh edition updates the discussion of consumer functional response by introducing alternative models based on the ratio of prey to predator numbers

rather than prey density per se. This discussion is coupled with reviews of experimental and field studies that support the ratio-dependent models.

The present edition connects ratio-dependent models of functional response to patterns of consumer abundance and secondary production in ecosystems. Previous editions have provided thorough coverage of the ecology of primary production in terrestrial and aquatic ecosystems, but secondary production has received much less attention. This seventh edition addresses this deficiency by including a section that covers the fundamentals of secondary production. The introduction to secondary production in this edition is presented in the context of consumer responses to variations in primary production.

New supplementary materials are placed online. Materials cut from the sixth edition and those previously cut from the fifth and fourth editions are available online. Suggested readings have been updated and placed online, along with answers to Concept Review and Critiquing the Evidence questions.

Significant Chapter-by-Chapter Changes

In **chapters 1 to 23**, numbered learning outcomes were added to all concept discussions and Evaluating the Evidence and Applications features. The average number of learning outcomes added to each chapter is 20.

In **chapter 10**, a new Applications feature explores evidence that plant and animal ranges have shifted northward and to higher latitudes in the Northern Hemisphere during the recent period of rapid global warming. This is the beginning of the global climate change thread in the seventh edition. However, the presentation builds on earlier content in chapter 1 on population responses to climate change, including evolutionary responses, and in chapter 4 on temperature relations of organisms.

In **chapter 12**, a new Applications feature reviews studies that have shown shifts in the timing of flowering in plants and of migration in birds in response to climate warming. The discussion complements the earlier discussion of shifts in species ranges in chapter 10 by demonstrating that climate warming is not just inducing organisms to move in response to global warming but also adjusting their life histories.

In **chapter 13**, the Lotka-Volterra equations have been modified from previous editions to make them more standard, less cluttered, and easier for students to follow, which is essential, since these equations are the foundation of the mathematical ecology covered in the text.

In **chapter 14**, we revisit predator functional responses first introduced in chapter 7 by evaluating alternatives to those models. The Lotka-Volterra models of predator-prey interactions published in the early twentieth century stimulated a long line of research. More recently, researchers have offered alternatives that help identify where those classical mathematical models, with their simplifying assumptions, apply and where alternative formulations better account for aspects of predator-prey interactions, particularly at larger spatial and longer temporal scales. The discussion in this chapter reviews how recent ratio-dependent functional response models better predict predator

functional responses in experimental and natural settings. The discussion helps to dispel the idea that mathematical ecology ceased to develop in the mid-twentieth century and reinforces the complementary roles of theoretical, experimental, and observational studies.

In **chapter 18**, a new concept connects primary producer diversity to higher levels of primary production. The chapter also includes a new concept featuring the relationship between levels of primary production and secondary production. This discussion provides a basis for introducing the fundamentals of secondary production. This addition also revisits the ratio-dependent functional responses introduced in chapter 14 by extending the implications of those models beyond predator functional response to the trophic structure of ecosystems. The treatment also formally introduces secondary production, filling a conceptual gap in previous editions.

In **chapter 20**, the fields of ecological restoration and restoration ecology are introduced for the first time. Human impact on the environment has altered ecological communities and ecosystems in nearly every corner of the planet. Restoring

structure and function to these systems emerges as one of the great contemporary ecological challenges. Increasingly ecologists addressing this challenge are turning to the conceptual framework of ecological succession to guide their work. Examples of such work are included in this chapter to help bridge the historical divide between ecological theory and restoration practice.

In **chapter 23**, the discussion of the Antarctic ozone hole has been updated to 2013, including 35 years of data from NASA on the size of the ozone hole. The pattern shows that the maximum size of the Antarctic ozone hole has stabilized, signaling a basis for ozone recovery predicted by atmospheric scientists over the next 50 years, providing a bit of good planetary news. The growing body of climate change research, published since the earlier editions of *Ecology Concepts and Applications*, has greatly improved understanding of how earth's changing climate will impact ecosystems and human populations, if not stabilized. A discussion of these impacts concludes this edition, underscoring the relevance of ecological knowledge to sustaining natural as well as human-centered systems.

Abbreviations Used in This Text

°C	degrees Centigrade	Ψ_{matrix}	reduction in water potential due to matrix forces within plant cells	V_E	variance in phenotype due to environmental effects on the phenotype
‰	grams of salt per kilogram of water	Ψ_{pressure}	reduction in water potential due to negative pressure created by water evaporating from leaves	V_T	total variation
λ	geometric rate of increase	Ψ_{soil}	water potential of soil	V_{GE}	variation due to gene-by-environment interactions
kPa	kilopascal	Ψ_{plant}	water within plant cells	V_R	unexplained residual variation
MPa	megapascal			X	independent variable
N	newton	δX	\pm the relative concentration of the heavier isotope, for example: D, ^{13}C , ^{15}N , or ^{34}S in ‰	Y	dependent variable
Pa	pascal			a	Y intercept
cm	centimeter	H_s	total heat stored in the body of an organism	b	regression coefficient; slope of the line
cm^2	square centimeter	H_m	heat gained from metabolism	PCR	polymerase chain reaction
cm^3	cubic centimeter	H_{cd}	heat gained or lost through conduction	R_0	net reproductive rate
g	gram	H_{cv}	heat lost or gained by convection	T	generation time
kg	kilogram	H_r	heat gained or lost through electromagnetic radiation	r	per capita rate of increase
mg	milligram	H_e	heat lost through evaporation	I_{max}	maximum per capita rate of increase; intrinsic rate of increase
mg/L	milligrams per liter	$\text{MgH}_2\text{O/L}$	milligrams of water per liter	N	population size
$\mu\text{g/L}$	micrograms per liter	$\text{MgH}_2\text{O/m}^3$	milligrams of water per cubic meter	N_t	number of individuals at time t
Tg	terragrams	$\text{gH}_2\text{O/m}^3$	grams of water per cubic meter	N_0	initial number of individuals
ha	hectare	W_d	water taken by drinking	e	base of natural logarithms
km	kilometer	W_f	water taken in with food	χ^2	chi-square
km^2	square kilometer	W_a	water absorbed from the air	O	observed frequency of a particular phenotype
km^3	cubic kilometer	W_e	water lost by evaporation	E	expected frequency
m	meter	W_s	water lost with various secretions and excretions	K	carrying capacity
m^2	square meter	W_r	water taken from soil by roots	GSI	gonadosomatic index
m^3	cubic meter	W_t	water lost by transpiration	N_1 and N_2	population sizes of species 1 and 2
μm	micrometer	W_i	internal water	K_1 and K_2	carrying capacities of species 1 and 2
mm	millimeter	PEP	phosphoenolpyruvate	$r_{\text{max}1}$ and $r_{\text{max}2}$	intrinsic rates of increase for species 1 and 2
nm	nanometer	PGA	phosphoglyceric acid	s_x	standard error
μmol	micromole	RuBP	ribulose biphosphate	s	sample standard deviation
L	liter	NH_4^+	ammonium	N_h	number of hosts
ml	milliliter	NO_2^-	nitrite	N_p	number of parasites or predators
μl	microliter	NO_3^-	nitrate	α	significance level
Ca^{2+}	calcium ion	Fe	elemental iron	μ	true population mean
Cl^-	chloride ion	Fe^{2+}	ferrous iron	t	value of the statistic t , either calculated or determined from a Student's t table
Fe	iron	CO	carbon monoxide	H'	the value of the Shannon-Wiener diversity index
K	potassium	P_{max}	maximum rate of photosynthesis	p_i	the proportion of the i th species
Mg	magnesium	I_{sa}	irradiance required to saturate photosynthesis	\log_e	the natural logarithm
Mg^{2+}	magnesium ion	N_{e1}	number of prey 1 encountered per unit of time	kcal	kilocalories
N	nitrogen	E_1	energy gained by feeding on an individual prey 1 minus the costs of handling	R_{sample}	the isotopic ratio in the sample, for example, $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$
Na	sodium	C_s	cost of searching for the prey	R_{standard}	the isotopic ratio in the standard, for example, $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$
Na^+	sodium ion	H_1	time required for "handling" an individual of prey 1	m_t	mass of leaves at time t
P	phosphorus	S^2	sample variance	m_0	initial mass of leaves
AET	actual evapotranspiration	RAPD	randomly amplified polymorphic DNA	e	base of the natural logarithms
PAR	photosynthetically active radiation	h^2	heritability of a trait	k	daily rate of mass loss
°S	degrees south	V_G	genetic variance	U	Mann-Whitney statistic
°N	degrees north	V_P	phenotypic variance	CFC	chlorofluorocarbons
CPOM	coarse particulate organic matter				
FPOM	fine particulate organic matter				
PDSI	Palmer Drought Severity Index				
MEI	metabolizable energy intake				
\bar{X}	sample mean				
n	sample size				
ΣX	sum of measurements or observations				
Ψ	water potential of a solution				
Ψ_{solute}	reduction in water potential due to dissolved substances				

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