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Dissecting and Reconstructing Time and Space for Replicable Biological Research

Barbara Helm and Ayelet Shavit

Precise locations from global positioning systems and exact times from atomic clocks are often insufficient and potentially misleading attributes of an organism's movements or physiology. A close look at autocorrelation of repeated samples can indicate the potential for successful replication and help us to identify relevant patterns in space and time. Appreciating the many components of space and time and accounting for their combined effects on data will improve the replicability of observational and experimental studies.

"Time" and "space" are two fundamental dimensions in the characterization of processes and objects in the life sciences, and therefore, clear and unambiguous temporal and spatial information is a prerequisite to biologically meaningful replication. Given the availability of high-precision atomic clocks and global positioning systems, it may seem straightforward to return to the same point in space and to identify an equivalent point in time for the sake of observational or experimental repetition. However, even with high-precision technology, measurements and descriptions of time and space are neither accurate nor unambiguous for repetition and subsequent generalization. Consequently, repeating a laboratory manipulation or field survey at an approximately equivalent

233

location in time or space can be a cause for additional variation and error, sometimes with substantial impacts.

In this chapter we draw attention to the importance of careful consideration of time and space for meaningful replication. As a first step, we show that seemingly straightforward assumptions about variation over time and space do not hold. Instead, the many aspects that contribute to an organism's time and space lead to substantial ambiguity and often incompatible practice. In order to tackle this ubiquitous problem, we view the operational meaning of "time" and "space" from three different perspectives—exogenous, endogenous, and interactionist—which we argue should not be conflated. We then illustrate the implications by presenting in a single table a wide range of paradigmatic examples grouped by spatiotemporal descriptors and reviewed sequentially from all three perspectives. Given the fundamental role of spatiotemporal information for repeating biological observations or experiments and its ubiquitous ambiguity, we conclude that such a reconstruction of "time" and "space" within a general, pluralistic, and multi-faceted table is not only new but also a first important step to be further developed. After all, our aim is to encourage further thought about appropriate measurements of time and space. We are convinced that replication of studies can gain substantially from recognizing and teasing apart different aspects of time and space instead of using a single universally standardized concept.

AMBIGUITIES OF TIME AND SPACE: PATTERNS OF VARIATION

Variation over time and space affects replication in many ways. The title of this book refers to a common interpretation of Heraclitus's (allegorical) insight that one can never step twice in the same river. One would tend to assume, however, that stepping into the river twice within very little time or space would make the events relatively similar. Generally, the closer in time or space that two sampling events occur, the more similar, and thereby the more repeatable, they will be expected to be. This expectation holds for some, but not all, biological patterns and processes (for useful contrasts, see Chapters 6–8 and 15).

The change in similarity between observations at increasing temporal or spatial distance (i.e., the temporal or spatial "lag") can be quanti-

fied by an autocorrelation function (ACF; Fig. 16.1).[1] The different forms of ACFs observed in biological data introduce some of the difficulties associated with replication. Importantly, there is wide variation in the form and distribution of the ACF, with substantial implications for repeatability and experimental design. The most extreme situation is no autocorrelation over time and space (see fig. 16.1, *panel A*), so that subsequent samples are statistically independent, implying that their similarity does not depend on their measured positions in time or space. However, some autocorrelation is commonly detected. In this chapter we emphasize ambiguities in time because ambiguities in space are discussed in general in Chapter 15 and elsewhere in greater detail.[2]

Some biological processes proceed directionally through time. In these instances, time is seen as continuous and directional, starting from an arbitrary point and proceeding through successive (and cumulative) elapsed time units (e.g., seconds or years). Biological processes that change directionally include the development and aging of organisms and stages of succession toward climax community. In such cases, repeated samples will become progressively more dissimilar to each other and the ACF may decay through time. Accounting for the change in the ACF in sampling or experimental protocols or by post-hoc analytical techniques would seem straightforward. However, the rate of decay may vary (see fig. 16.1, p*anel B* and *panel C*), for example, between sites or individuals, and the factors that shape specific trajectories, for example, those of development and aging, are not completely known to researchers. Therefore, introducing a common correction factor can in fact introduce artifacts and reduce repeatability.

Differences in trajectories of development and aging are so relevant that researchers have introduced definitions of time that are alternatives to the passage counted in seconds or years. For example, data collected from growing individuals are often reported relative to sequential stages, without explicit reference to the passage of time.[3] Furthermore, growth rates of many organisms, for example, fish, are greatly influenced by ambient temperature, which often differs between studies and replicates.[4] In yet another convention, therefore, the time taken for growth is sometimes reported relative to cumulative ambient temperature, such as degree days (i.e., integrals of a function of time and concurrent ambient temperature). Similarly, in agricultural and ecological studies, the
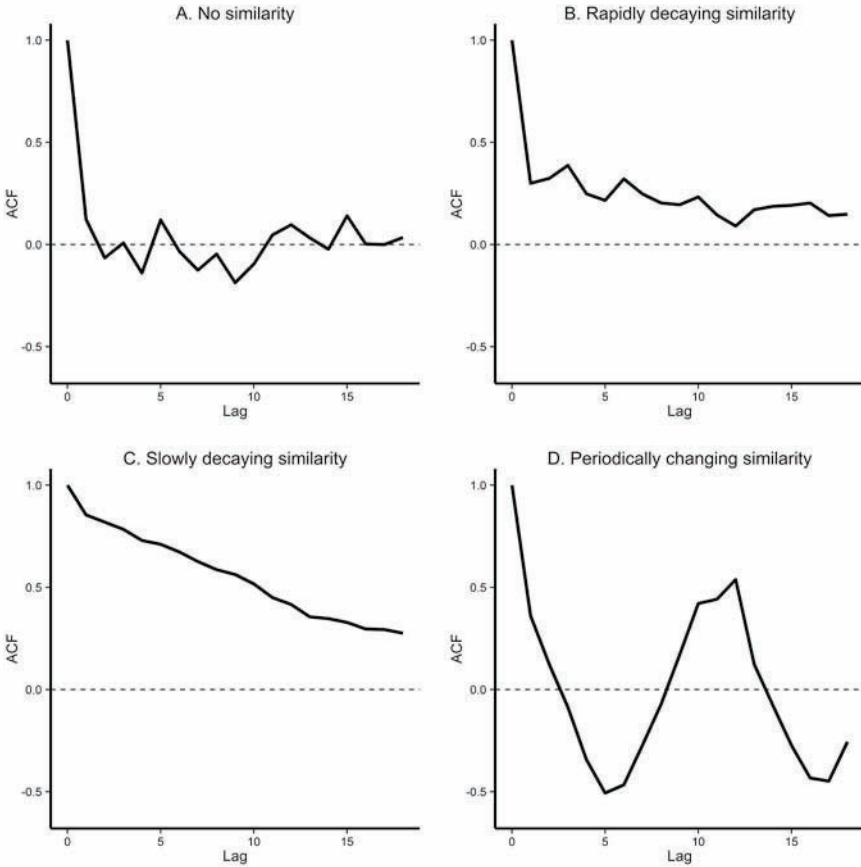
FIG. 16.1. Simulated changes in similarity over successive observations, as measured by an autocorrelation function (ACF). Simulated data and calculations were generated using the ACF in the stats library of the R software package (R Core Team 2015), with the kind support of Iain Malzer. The graphs show for four scenarios how the similarity of sequential observations declines with sampling intervals ("lags") over time and space. The ACF assumes values between 0 (no similarity), indicated by the dashed horizontal line, and ±1 (complete similarity); note that for lag=0 the ACF is always 1. *Panel A:* No similarity (successive observations are independent of one another). *Panel B:* Rapidly decaying similarity. Some similarity, but ACF decays rapidly over sampling intervals. *Panel C:* Slowly decaying similarity. Initially high similarity, with ACF decaying slowly through time. *Panel D:* Periodically changing similarity. Periodic processes may show a rapid decline in ACF followed by a subsequent rise. Here, the time between peaks is 12 observations, potentially representing monthly samples from an annual process.

progress of seasonal processes is often related to degree days, which are calculated in multiple ways and are used, for example, to time agricultural interventions such as the use of pesticides.[5] In such cases, the clock and calendar time of a given experiment can be reconstructed by other researchers only if the starting date and ambient temperatures are reported. Although these conventions have doubtlessly practical advantages, the fact that multiple definitions of time can often not be translated between studies presents methodological challenges and may limit comparisons, meta-analysis, or even spatiotemporally defined repetition.[6] In effect, "time" in these biological processes is not unambiguously and objectively captured by a clock or calendar.

The age of an organism may be similarly ambiguous. Conventionally reported in cumulative counts (e.g., of days following events like fertilization or birth), the biological implications of a given age (i.e., aging) differ between species and between individuals within species. The aging of animals, for example, may proceed more quickly under severe environmental or developmental conditions (see fig. 16.1, *panel B* versus *panel C*).[7] Therefore, the chronological age of an organism, measured in time units since birth, is sometimes distinguished from its biological age, measured by biomarkers associated with physiological processes of aging (see also Chapter 10). The ambiguities of clock and calendar time can reduce the success of replication. For example, if a pharmacological trial involves the re-sampling of mice, doing so after a fixed interval of 100 days seems like an accurate protocol, but differences in individual rates of aging may inflate variation in the outcome (see also Chapter 10). Likewise, if populations of wild animals aged at different rates, their population dynamics could differ because of age-dependent fertility.[8] These problems are not easily resolved because clear biomarkers are rarely available and few studies simultaneously report both chronological and biological age.

When dealing with spatial patterns, it is common to assume that the closer two sampling events are located to each other, the more similar they are to one another. As with analyses of time, spatial autocorrelation generally decreases with distance (i.e., spatial lag) and likewise can be quite variable (see fig. 16.1, *panel A* versus *panel C*).[9] For example, samples collected over short distances but over steep elevational gradients can be very different from one another. Conversely, samples from

similar elevations at distant locations (e.g., high-elevation alpine habitats) might be more similar than those from surrounding lowlands, indicating that altitude explains more variation than the distance separating samples.[10]

Even if, in this example, elevation is accounted for, samples or populations from neighboring locations may differ depending on exposure, landscape patch structure, or phylogenetic history.[11] Such obvious examples stand for various other, more subtle, factors that influence the trajectories of spatial autocorrelation. Awareness of these difficulties has resulted in a duplication of space in ecological literature by distinguishing between geographic space (e.g., latitude, longitude) and environmental space (e.g., environmental resources).[12] This duplication is not easily harmonized, as is evident from a study in which biologists from different backgrounds were actually observed and later interviewed.[13] When the researchers were asked to describe both geographic and environmental space, their options became mutually exclusive: there was no single location that fit both descriptions. When working in the field, on the smallest spatial scale, they typically sought to relocate the measurement using a particular device (e.g., a global positioning system [GPS] for measuring geographic space or a pitfall trap for measuring environmental space) to improve the accuracy (often considered to be synonymous to realism) or the representativeness (i.e., generalizability) of the location in space of an organism.[14] In effect, more precise GPS machinery revealed—and in that sense increased—this instance of incommensurability rather than solving it.[15]

Patterns of variation in nature often are periodic rather than (or in addition to) being directional. Accordingly, although the similarity of successive replicates is expected to decrease with the passage of time, it will subsequently increase again (see fig. 16.1, *panel D*). Such periodic processes often relate to geophysical cycles, which arise from movements of the Earth and the Moon around the Sun, and are highly precise and predictable.[16] Chronobiology, the systematic study of adaptations to geophysical cycles, has elaborated that annual and daily, as well as lunar and tidal, cycles fundamentally shape the distribution, behavior, physiology, and gene expression of most, if not all, organisms on earth.[17] Geophysical time scales act in combination with one another. For example, there can be a high probability of encountering an organism in a

given state or at a given location depending on a particular combination of phase of solar year, phase of lunar cycle, and time of day.[18] In addition, periodic processes also occur on time scales that are shorter or longer than geophysical cycles and are hence harder to predict. Examples include very short (ultradian) rhythms such as activity bouts of rodents, and longer-term rhythms, including population cycles and the North Atlantic Oscillation (NAO).[19] Repeatability of observations or experiments can be improved if the period and phase of variation in the distribution or state of an organism are taken into account.

Such accounting, however, is also not always straightforward. For example, although dependent on the same geophysical cycle, tidal cycles differ in phase between coasts.[20] Even individuals within species can differ in the phase of their periodic activities (i.e., they have individual chronotypes) or change phase over time, both of which increase variation among replicates and among repeated samples.[21] Additional ambiguity arises from effects of latitude and from precession of geophysical cycles, such as differences in the times of sunrise and sunset across the solar year and among locations.

Organisms often change their activity patterns accordingly, adding complexity to spatial or temporal replicates. For example, sampling of birds during the dawn chorus at a set time in different locations may yield completely different population estimates or assessments of physiology.[22] Researchers might need to decide whether replicates should be carried out according to clock time, light intensity, or the birds' local behavior.

Similar ambiguity applies to periodicities that are not directly linked to geophysical cycles. Population cycles, like those of muskrat and mink, typically differ in phase between locations and often show highly variable periodicities, making suitable replication of a population study very difficult to define.[23]

Anthropogenic changes to natural environments are adding further challenges in accounting for periodic processes. For example, the fast spread of urban sprawl is changing the light environment, and thereby the implication of "night," for increasing numbers of wild organisms.[24] Similar reasoning applies to annual cycles. For example, annual reproduction can differ in timing between years, depending on weather. At present, global climatic change is shifting the timing and progress of annual events (e.g., phenology) in ways that vary across space.[25]

Climatic change affects different organisms differently, so that on a given date in any particular year (e.g., 1 May) components of both the abiotic and the biotic environment may be in different phases relative to earlier studies and to one another. For example, birds that return from migration on the same day may in some years miss the vegetation flush or peak availability of food.[26] Therefore, ecologists have suggested that it may be more informative to relate phenological events, such as timing of reproduction, to variables such as abundance of food instead of solely to clock and calendar time.[27] When data are reported relative to biotic components of time, ecological "distance" (i.e., the "lag" in fig. 16.1) might replace descriptors derived from clocks or calendars. Clearly, without thoughtful choice, comprehensive recording, and translational efforts, the ambiguities pointed out earlier can result in loss of precision and poor success of replication.

COMPONENTS OF TIME AND SPACE: THE IMPORTANCE OF CONCEPTUAL PERSPECTIVES

The many aspects that contribute to the spatiotemporal location of an organism or biological processes collectively determine the probability of its occurrence, the number of individuals present, or its physiological state. Importantly, different fields of biology differ in the emphasis placed on the various aspects in space and time that are studied, in the data collected, and in the ways of quantifying and reporting the data. These differences arise from different conceptual approaches to the study of organisms that are inherent to different research fields and from different criteria—or different priorities among the same criteria—for evaluating the quality of the research and/or data (i.e., epistemic values). However, these differences rarely are reflected explicitly. Whereas all aspects potentially matter, a biologist's concept of time and space affects those aspects that are noted and consequently will inform the design of replicated observations and experiments or repeated studies.

We attempt (table 16.1) to give an overview of aspects of an organism's time and space, grouped into descriptors analogous to commonly used terms in ecology and environmental science (abiotic, biotic, interspecific, intraspecific). We associate these descriptors with three conceptual perspectives, each of which has specific value and meaning in different fields within the life sciences. Hence, these descriptors can be

Table 16.1

Components of time and space that collectively affect the distribution and physiological state of organisms, viewed from three general perspectives: A. exogenous, B. endogenous, and C. interactionist

	TIME	SPACE
A. Exogenous perspective		
Abiotic components		
Unique identifier	Continuous counts from a conventionally set starting point (e.g., religious traditions, software conventions)	Conventional coordinates of latitude and longitude, prime meridian in Greenwich, UK
Underlying geophysical properties	Movements of Earth and Moon, Earth's offset axis: solar annual, diel (daily), lunar, and tidal cycle	Rotational axis of Earth, properties of sphere; location on sphere relative to Earth's axis
Other abiotic components	Environmental seasonality, e.g., long-term temporal patterns of climate, temperature, snow cover, precipitation, etc.; phase of fluctuation in atmospheric pressure; integrals of abiotic factors, e.g., degree days	Elevation/depth, slope, exposure; magnetic field; long-term climate, wind and sea currents
Shared abiotic components	Weather: current local temperature, snow cover, precipitation, humidity, etc.	
Biotic components		
Interspecific biotic components	Timing of other species, e.g., NDVI (normalized difference vegetation index), foliage, progress of agricultural practice, state of succession, predator activity, parasite cycles, food availability	Habitat, species composition, land use, predator density, pathogen load, food availability
Intraspecific biotic components	Activity and state of conspecifics (e.g., flock formation, reproductive state), phase within population cycles	Population density, location relative to lineage, location relative to center of population distribution

(continued)

Table 16.1 (Continued)

	TIME	SPACE
B. Endogenous perspective		
Abiotic components		
Unique identifier	Age (time elapsed, e.g., from birth)	Home (place of origin); destination (e.g., of
	Phase (biological clock time of a defined central pace- maker in the brain)	migration)
Internal properties that determine implications of abiotic components	Endogenous biological timekeeping, with periodicities of annual, diel, lunar, and tidal cycle	Memory of home roost, hibernaculum, wintering site, foraging patch, etc., relative to current position; arguably, internal map
Abiotic properties used as reference for the internal perception	Photic, thermal, gravitational, and other cycles or cues	Photic, geo-magnetic, chemical-gradient, and other cues
Other abiotic components	Temperature, snow cover, precipitation relative to energy supplies, time of resting, available shelter, etc.	
Biotic components		
Internal determinants of implications of interspe- cific components	Perceived predation risk (e.g., fear), experience of site and time of flowering (time and place learning), susceptibility to parasite (e.g., locally acquired antibod- ies; seasonal immuno-suppression)	
Internal determinants of implications of intraspe- cific components	Developmental stage, life-cycle stage, energy reserves, perceived progress of migration; hormonal conse- quences of social interactions affecting presence and physiology	

C. Interactionist perspective

Abiotic components

Unique identifier	None	None
Geophysical components resulting from organism's activities	Photic environment as chosen by an organism (e.g., through migration or avoidance of artificial light)	Latitude and longitude as chosen by an organism (site of coral or of migratory stop-over)
Other abiotic components	Temperature, snow level and precipitation of an organism's constructed microhabitat (e.g., depth and micro-climate of a burrow or nest); tidal height selected by timing of foraging trip	

Biotic components

Interspecific biotic components	Pathogen load as a consequence of behavior, food availability inside constructed microhabitat; temporal niche partitioning relative to predators or competitors	
Intraspecific biotic components	Self-selected population density; mating status; location, timing, and size of foraging group, experience based on learning, prospecting, eavesdropping, and information sharing	

Note: The entries for time and space are intended as illustrative examples, not as an all-inclusive list. Note that several components relate, to different degrees, to both time and space, and are therefore sometimes in a combined entry. For each perspective, entries are ordered from abstract and geophysical to increasingly organism-centered components.

associated with different notations and descriptions (see table 16.1, A–C). We call these perspectives exogenous, endogenous, and interactive. For each perspective, the table is arranged to progress from abstract and geophysical to increasingly organism-centered descriptors.

Exogenous perspective. In the first sense (see table 16.1, A), the location in space and point in time of a manipulation or survey is a framework outside of (exogenous to) the organisms and populations of scientific interest. At one extreme are abstract notions of time and space that are based purely on conventions, such as geographic coordinates based on a system of grid lines conventionally located with respect to the Earth's poles, the Equator, and Greenwich, England, as prime meridian, and time counted from an arbitrary starting point (e.g., the date coded as the number of full days since midnight of 1 January 1900 plus the number of hours, minutes, and seconds for the current day in Microsoft Excel or since January 1904 in Macintosh).

Although there may be good biological reasons for the occurrence of organisms at a given point in time and location in space, we tend to place them in this framework regardless of their specific interests, behavior, or metabolism. The time points and spatial locations denoted by these unique identifiers can then be detailed by further exogenous, abiotic quantifiers. These include latitude and longitude, used separately to characterize gradients; elevations above or below sea level, measured on an arbitrary date; year, day, hour, minute, and second, conventionally decided with respect to Earth's astronomical position relative to the sun; or temperature and other weather factors, measured at times and locations that to some degree relate to the observational or experimental situation.

Some biotic components of time and space also are exogenous in the sense that they are external to the organism, and they capture the context that may be relevant to a specific organism or population, for example, the composition of vegetation or its phenological state. For an organism's time, biotic information, such as the state of vegetation, may be highly relevant, but it rarely is quantified directly. As a shortcut researchers often use indices from remote sensing, such as the normalized difference vegetation index (NDVI).[28] Such indices have to be interpreted with caution: for example, the "greenness" that may be relevant for an ungulate or insectivorous bird may not be apparent from NDVI values,

which in turn might reflect the greenness of evergreen tree cover. Likewise, specific biotic features, such as the phenology of a specific host plant or food item, may be a centrally important temporal aspect, whether or not researchers are aware of it. Intraspecifically, a wide range of factors can affect spatiotemporal patterns of distribution and state, for example, availability of a flock or a mate.[29]

Commonly, in spatial analyses, abiotic and biotic information is added in subsequent analytic procedures using well-defined layers in a geographical information system (GIS).[30] As described earlier, ecologists are well aware that there is a crucial ecological dimension to an organism's presence in a geographical location and that, in view of geographical and ecological heterogeneity, proximity in latitude and longitude does not ensure similarity.[31] Hence it may seem to follow that geographic coordinates together with GIS layers can define a location that will suffice for repeatability.

However, this implicit assumption adds uncertainty of its own. Even before adding ecological layers, the geographical coordinates themselves go through a complex georeferencing process, and to estimate its uncertainty one must also record, in the field with a GPS device, the extent, accuracy, and datum of the instrument.[32] Estimates of elevation are also uncertain, as they may be determined either by local barometric pressure or by internal topographic maps. Finally, adding GIS layers of habitat or soil type to more accurately describe a location is far from being globally standardized, and their uncertainty is often not comparable among maps used in different studies. These gaps and uncertainties can be taken into account in statistical models of occupancy and detectability (see Chapter 15); such models are improved with additional specification of how time and space were described throughout the research project and subsequent data management (see Chapters 13, 14). The addition of written narratives and standardized photographs of study sites and times (see Chapters 4, 5) also can be helpful while being open to individual interpretation.

Endogenous perspective. At the other extreme is a concept that is focused on the internal representation of time and space by an individual organism (see table 16.1, B). The presence of an organism, or the state it is in (e.g., reproducing, migrating), may be better understood and described relative to the home range or destination of the organism, to its age, or to a phase in its daily or annual cycle. Likewise, in an experiment,

physiological measurements such as the immune response or performance of a study organism may differ depending on an individual's age and circadian clock phase, even if exogenous conditions are identical (see also Chapters 9, 10).[33]

The basis for this organism-centered perspective is an awareness of the importance of physiological and genetic disposition, on the one hand, and of internal representations of time and space, on the other. As explained earlier, many biological processes are scaled to geophysical properties that thereby influence the probability of encountering an organism or of finding it in a specific physiological condition. Because these properties are highly predictable, organisms have evolved internal representations of time and space that direct their behavior and prepare them for upcoming conditions.[34] These internal representations exist separately from external conditions but use the latter as references or cues, so that temporal and spatial behavioral or physiological processes are a combination of internal and external factors.

For example, biological rhythms persist even in completely constant environments, with periodicities close to, but slightly different from, those of corresponding geophysical cycles. Even under captive, constant conditions, animals may orient themselves spatially toward seasonally appropriate destinations or home areas.[35] Internal rhythms may not align fully with environmental predictors. For example, a hibernating species may be active before environmental predictors suggest that it should be, because, based on its internal clock, it may have already emerged from its hibernaculum.[36] Likewise, the presence of a migratory bird in the Sahara Desert may be inferred from knowledge of its migration route and energetic state but not from local exogenous features.[37]

Differences between exogenous and endogenous perspectives can be found for many identified descriptors of time and space (see table 16.1A and B). For example, even occasional predator attacks may change population dynamics and patterns of use of time and space because of perceived predation risk.[38] Ignoring internal mechanisms such as cognitive maps, spatiotemporal effects of experience, memory, and habituation in analysis and modeling have been linked to deviations from predictions and are known to complicate interpretation and replication.[39] As in the case of exogenous factors, considering and documenting endogenous variables can improve the replication of research.

Interactionist perspective. The third intersecting perspective of time and space, which we term interactionist, takes account of the configuration of aspects of time and space by the organisms themselves (see table 16.1, C). This organism-centered approach views the spatiotemporal environment as being dynamically constructed by the actions of organisms over time. Their physiology, metabolism, and in particular behaviors, such as habitat choice, nest building, singing, or feeding, partly define their space and time.[40] In this sense, space and time also become the product of the interaction of the organisms with their environments.

Organisms modulate or configure their spatiotemporal environment through physical interference or movement, among many other activities. For example, the nests and burrows that many organisms construct often lead to temperature and light conditions that differ substantially from those recorded outside and therefore from information derived from GIS layers. Likewise, the choice of a nesting site can affect the reproductive condition as well as the daily and annual timing of a bird.[41] A migratory bird's choice of a wintering area, because of day length or nutritional conditions it encounters, can alter its timing, state, and breeding performance in the ensuing spring in ways not anticipated from local conditions.[42] Cultivation of fungi or storage of food may alter nutrient availability, and consequently population dynamics, but these factors and their effects on replication are not easily captured in ecological surveys and are frequently ignored by species distribution models.[43]

TOWARD RESOLVING AMBIGUITIES OF TIME AND SPACE

Biologists and biological disciplines differ in their concepts of time and space. Community ecologists and biodiversity conservationists normally emphasize exogenous factors; population ecologists and behavioral biologists sometimes focus on interactionist factors; and physiologists may pay closest attention to endogenous factors. All scientists seek to generate results that are generalizable and will be applicable to a wide range of questions, species, times, and places. Yet the difference between concepts of time and space, along with their corresponding research perspectives, can introduce ambiguity and reduce the likelihood of accurately repeating an experiment or observation.

Ignoring the different meanings that denote time and space in one's study is likely to result in empirical gaps and mistakes, whereas proactively minding the gaps within each conceptual domain can avoid much of the ambiguity. Resolving the tension requires a more inclusive view that will accommodate more divergent data fields of space (or location) and time on the gradients between the exogenous, endogenous, and interactionist perspectives. We recommend that, where possible, researchers use more than one data model for measuring time and space while keeping track of the variance between the findings from the different data and models (see also Chapters 9, 10, 15 and 17).

To be both specific and general, we suggest six steps one can follow in order to improve the repeatability of observations or experiments. First, be aware of spatiotemporal complexity and diversity. Second, inclusively record such information across its conceptual gradient. Third, if possible, increase sample size and measurements of independent replicates to improve estimates of variability and connectivity of time and space (see Chapters 9, 10, 15). Fourth, record the history of the data and the metadata (see Chapters 13, 14). Fifth, be aware of, and optimize where possible, trade-offs between protocols linked to different concepts of time and space before starting a research project (see examples in Chapters 6–14). Finally, quantify and model the uncertainty as part of assessing data quality (see Chapters 13–15). Although these six steps will not entirely solve the problem of perfect replication over time and space, they provide an excellent start.

NOTES

1. Cressie and Wikle (2011).
2. Shavit and Griesemer (2009, 2011a, 2011b).
3. Schmidt and Starck (2010).
4. Chezik et al. (2013).
5. Rodríguez Caicedo et al. (2012).
6. Chezik et al. (2013).
7. Heidinger et al. (2012); Barrett et al. (2013); Mizutani et al. (2013); Jones et al. (2014).
8. Hammers et al. (2012).
9. Spatial autocorrelation functions normally are displayed as semi-variograms but are directly analogous to temporal autocorrelation plots. See Cressie and Wikle (2011) for additional detail.
10. Körner (2003).

11. Moore et al. (2005); Warren et al. (2014).

12. Gaston et al. (2008).

13. Shavit and Griesemer (2009); Shavit (2016).

14. Here we accept Weisberg's (2006) interpretation of Levins's (1966, 1968) work on modeling strategies in ecology and his claim that Levins uses "accuracy" as if it were synonymous with "realism."

15. Shavit (2016).

16. Foster and Kreitzman (2005).

17. DeCoursey (2004); Foster and Kreitzman (2005); Tessmar-Raible et al. (2011); Numata and Helm (2014).

18. Helm et al. (2012); Zantke et al. (2013).

19. Halle and Stenseth (2000); Haydon et al. (2001); Hueppop and Hueppop (2003); Bloch et al. (2013).

20. Kaiser (2014).

21. Roenneberg et al. (2003).

22. Daan and Aschoff (1975).

23. Haydon et al. (2001).

24. Dominoni et al. (2013a, 2013b).

25. Visser et al. (2010).

26. Visser and Both (2005).

27. Ibid.

28. For examples, see Raess (2008); Tottrup et al. (2012).

29. Filchak et al. (2000); Visser and Both (2005); Helm et.al. (2006); Visser et al. (2010).

30. Store and Jokimäki (2003).

31. Gaston et al. (2008).

32. Wieczorek et al. (2004).

33. Roenneberg et al. (2003); Cermakian et al. (2013).

34. DeCoursey (2004). For examples, see Holland and Helm (2013); Cheeseman et al. (2014).

35. Gwinner and Wiltschko (1980).

36. Lane et al. (2012).

37. Biebach (1985).

38. Zanette et al. (2014).

39. Gremillet and Boulinier (2009); Ruxton and Colegrave (2010).

40. Oyama (1985); Ellison et al. (2005); Shachak et al. (2008).

41. Dominoni et al. (2013a, 2013b).

42. Gwinner and Helm (2003); Studds and Marra (2005).

43. Silva et al. (2003); Guisan and Thuiller (2005); Strickland et al. (2011).