





To improve ecological understanding, collect infection data

ALYSSA-LOIS M. GEHMAN ^{1,2,3,†} DARA A. SATTERFIELD ^{1,4} CAROLYN L. KEOGH,^{1,5}
ALEXA FRITZSCHE MCKAY ¹ AND SARAH A. BUDISCHAK ^{1,6,7,8}

¹Odum School of Ecology, University of Georgia, Athens, Georgia, USA

²Hakai Institute, End of Kwakshua Channel, Calvert Island, British Columbia, Canada

³Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

⁴Smithsonian Migratory Bird Center, Smithsonian Conservation Biology Institute, Washington, D.C., USA

⁵Department of Environmental Sciences, Emory University, Atlanta, Georgia, USA

⁶W. M. Keck Science Department of Claremont McKenna College, Claremont, California, USA

⁷W. M. Keck Science Department of Pitzer College, Claremont, California, USA

⁸W. M. Keck Science Department of Scripps College, Claremont, California, USA

Citation: Gehman, A.-L. M., D. A. Satterfield, C. L. Keogh, A. F. McKay, and S. A. Budischak. 2019. To improve ecological understanding, collect infection data. *Ecosphere* 10(6):e02770. 10.1002/ecs2.2770

Abstract. Ecologists seek to understand and predict how organisms respond to multiple interacting biotic and abiotic influences, an increasingly difficult task under anthropogenic change. Parasites are one of these biotic influences that are pervasive in natural systems and frequently interact with other stressors. Because they often have cryptic effects on their host organisms, their role in the distribution, abundance, composition, and dynamics of populations, communities, and ecosystems is easy to overlook. However, studies that neglect the role of parasitism may miss or misinterpret organismal responses to environmental change, hampering ecological predictions. We discuss case studies wherein the inclusion of parasite infection status altered the interpretation of ecological outcomes, and offer paths forward to make parasite data acquisition, analysis, and interpretation more accessible to ecologists. Given that parasites are responsive to environmental changes, timely attention to their influence on host responses is critical for accurately predicting future ecological states.

Key words: climate change; disease ecology; long-term data; parasitism.

Received 7 March 2019; revised 30 April 2019; accepted 1 May 2019. Corresponding Editor: Charles E. Mitchell.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** alyssamina@gmail.com

PARASITES: NOTORIOUS AND NEGLECTED, BUT NECESSARY

Ubiquitous and abundant, parasites influence ecological processes at all levels, from individuals and populations to communities and ecosystems. Parasites alter host behavior, shape host population dynamics, mediate species interactions, and influence energy flow through food webs (Selakovic et al. 2014, Decaestecker et al. 2015, Wood and Johnson 2015, Edeline et al. 2016, Jacquin et al. 2016). Yet, because their

effects are often cryptic, the influence of parasites on ecological processes is easy to overlook. Worryingly, ecological studies that neglect the role of parasitism may ultimately miss or misinterpret important patterns. This could hamper the accuracy of ecological predictions in the face of environmental change, particularly if organismal responses that are influenced by parasites are misattributed to other factors.

Ecologists already routinely measure and account for environmental covariates (such as temperature) that can mediate organismal

response variables of interest. Here, we argue that parasites can be one of these critical covariates, and we highlight several opportunities that could make quantifying parasites more accessible. We use the ecological definition of parasitism (i.e., a symbiosis where one species benefits while harming another), which includes parasites ranging from viruses to worms and ticks (Anderson and May 1978). Illustrating the danger of overlooking parasites, we present four case studies in which consideration of host infection status altered the interpretation of ecological outcomes. These examples highlight the crucial need to collect baseline data on parasite infection status of hosts to better understand organismal and population responses to global change. To facilitate broader inclusion of parasitological data in ecological studies, we offer paths to make parasite data acquisition, analysis, and interpretation more achievable for ecologists focused on other aims. We hope to motivate collaborations across disciplines to expand the consideration of parasites in ongoing and future ecological work.

EXCLUDING PARASITES: THE COST TO SCIENCE

The case studies we present here demonstrate the value of considering parasites in several fundamental ecological questions related to organismal performance, community interactions, and population dynamics.

Parasites modify herbivore–plant interactions

In the face of rapid climate change, understanding the effect of temperature on herbivore feeding rates is a topic of increasing importance (Mertens et al. 2015). The metabolic theory of ecology suggests that body temperature alters feeding rates (Brown et al. 2004). However, parasite infection also influences host feeding rates (Wood et al. 2007). Moreover, a case study of the marine snail *Littorina littorea* and their trematode parasites demonstrated that infection can interact with temperature to affect how herbivore feeding rates respond to warming (Larsen and Mouritsen 2009). Ignoring trematode infection (i.e., grouping all snail grazing data), the average grazing rate appeared to have increased with temperature (Fig. 1A). However, analyzing the data by infection status (Fig. 1A) revealed that uninfected snails retained the same grazing rate

regardless of temperature treatment, while infected snails increased their grazing rate at higher temperatures (Larsen and Mouritsen 2009). Thus, the overall population-level responsiveness of grazing rate to elevated temperatures should depend on parasite prevalence in the population (Lavery et al. 2017). This example highlights how studies of temperature effects on herbivory would benefit from considering the modulating effects of parasites.

Parasites shift the outcome of competition

Evidence suggests parasites can alter even the most fundamental of ecological processes structuring biological communities, such as competition between species. In competition experiments between two plankton species, *Daphnia magna* is strongly dominant to *Daphnia pulex* (Decaestecker et al. 2015). However, in the presence of bacterial and microsporidian parasites, *D. pulex* became the competitive dominant (Decaestecker et al. 2015). This reversal in competitive ability illustrates that parasites can be as important as predators in shaping community structure (Hutchinson 1961). However, unlike many predators, most parasites are not immediately detectable and could be heterogeneously distributed among study organisms or treatments. To reduce noise and avoid confounding results, parasites should be statistically accounted for by quantifying infection in field studies.

Parasites mediate invasive—native species interactions

In some cases, parasites can alter the mechanisms by which invasive species affect native flora and fauna—an important pattern for ecologists to note as the rate of species introductions increases around the globe (Seebens et al. 2017). When gray squirrels (*Sciurus carolinensis*) from North America invaded the United Kingdom, populations of native Eurasian red squirrels (*S. vulgaris*) declined precipitously. The reason for their declines was assumed to be direct competition, until evidence suggested that a parapoxvirus from (asymptomatic) gray squirrels was pathogenic for native red squirrels (summarized in Tompkins et al. 2002). Thus, parasites mediated the gray squirrel invasion (Tompkins et al. 2011). Early screening of invasive species for parasites with potential for transmission to

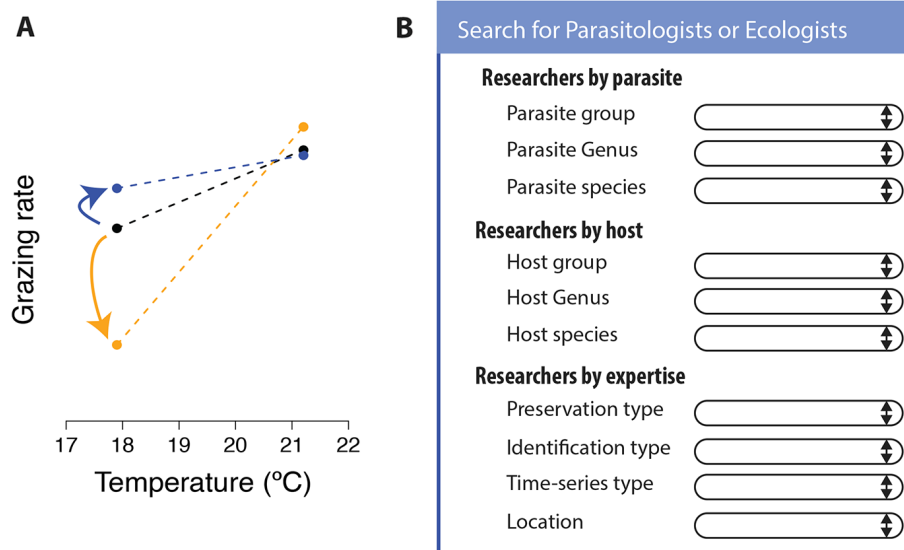


Fig. 1. (A) Grazing rates of *Littorina littorea* on *Ulva lactuca* at two temperatures with uninfected (dark gray; blue online) and infected snails groups (light gray; orange online) and a combination of both infected and uninfected snails (black; conceptually adapted from Fig. 3, Larsen and Mouritsen 2009). (B) Example of search terms proposed for a Web-based platform to facilitate collaborations between researchers with and without parasite knowledge.

native hosts could help predict or mitigate loss of native wildlife to invasive parasites.

Parasites explain unprecedented population declines

In recent years, catastrophic population declines of numerous wildlife species have alarmed ecologists and the general public. In some of the most familiar and striking examples, the cause of decline remained enigmatic until researchers explored parasite-related hypotheses. This was the case for die-offs of saiga (*Saiga tatarica*) in Kazakhstan (Kock et al. 2018), amphibian declines in Latin America (Kilpatrick et al. 2010), and shrinking colonies of little brown bats (*Myotis lucifugus*) in North America (Frick et al. 2017)—all of which have now been linked to parasites.

These dramatic parasite-mediated declines can sometimes illuminate the role of the host in its community. For example, on the North American Pacific coast, millions of sea stars across 20 species experienced mass mortality attributed to sea star wasting disease (Hewson et al. 2014). While the causative agent remains elusive, wasting symptoms have been associated with compromised microbial communities and viruses

(Hewson et al. 2018, Lloyd and Pespeni 2018). Extensive monitoring of marine invertebrates along the West Coast enabled researchers to detect and evaluate the effects of sea star wasting disease on hosts and their communities (Menge et al. 2016, Montecino-Latorre et al. 2016, Schultz et al. 2016, Burt et al. 2018, Miner et al. 2018, Moritsch and Raimondi 2018). The coast-wide decline highlighted new aspects of the ecology of affected sea stars, from unpredicted trophic cascades, to altered competitive outcome, to changes in prey size structure, zonation, and habitat use (Menge et al. 2016, Schultz et al. 2016, Cerny-Chipman et al. 2017, Gravem and Morgan 2017, Burt et al. 2018, Kay et al. 2019).

COLLECTING PARASITE DATA: THE WAY FORWARD

In an era of accelerating ecological change, the importance of providing historical baselines is increasing. Conducting baseline parasite surveys could revolutionize our ability to mitigate their conservation impact on host populations, to quantify risk of novel parasite invasion, and to utilize outbreaks as natural experiments for studying

community ecology of both free-living and parasitic species. While collecting exhaustive data on parasites may not be feasible in all research efforts, any additional collection of parasites or infection data will benefit our ability to understand past, present, and future ecological communities—of which parasites are undeniably a part—and their responses to changing conditions.

Examples of parasite monitoring in practice include the National Ecological Observatory Network (NEON, Springer et al. 2016), which is collecting data on pathogens of small mammals and mosquitoes, and the long-term ecological research (LTER) Sevilleta site, which has been collecting rodent parasite data since 1990 (Duszynski 2010). The One Health framework is expanding data collection from wildlife and domestic animals along with human populations, with recent calls for expanding the taxonomic scope of parasite sample collection (e.g., Leboeuf 2011, Schurer et al. 2016). In addition, several citizen science programs already incorporate parasite infection status in their sampling schemes (e.g., Monarch Health; FeederWatch; Chesapeake Bay Parasite Project; MARINe Sea star wasting syndrome observations). Long-term monitoring programs that already collect or sample organisms at regular intervals present ample opportunity for incorporating parasite data. For example, ecologists who coordinate LTER sites could recruit parasitologists to collaborate with annual or seasonal biological surveys. Smithsonian and Hakai Institute MarineGeo researchers identified new and exciting parasite species by including parasite specialists in their cohort of taxonomists conducting a BioBlitz on Calvert Island, British Columbia, Canada (catalogued on iDigBio, Appendix S1: Table S1).

Government scientists and wildlife biologists involved in surveying populations of imperiled species could non-invasively collect skin swabs, blood samples, or fecal samples to share with other scientists interested in monitoring for fungal parasites, blood parasites, intestinal helminths, and other infections (e.g., Justine et al. 2012, Franson et al. 2015, Torres and Kelley 2017, Carroll et al. 2018, Galbreath et al. 2019). Such samples could be collected and banked for future processing, in order to gather as much baseline information as possible (Bi et al. 2013, Galbreath

et al. 2019, Harmon et al. 2019). Further, the increasing capacity of sequencing technologies has expanded the value of non-destructive sample collection techniques and allows researchers to inexpensively archive samples in ethanol (Bi et al. 2013, Yeates et al. 2016). Newly developed eDNA techniques can make detection of free-living stages possible (Sengupta et al. 2019). Complementarily, whole organism sampling designs that preserve parasite type specimens for taxonomic ground-truthing could provide reference libraries of reliable DNA barcodes. As an additional option for infection data, some parasites (e.g., trematodes that cause black spot disease in fish; rhizocephalan infection in crabs) have externally visible signs of disease or infection which could be counted or photographed with minimal expense or expertise (Tobler et al. 2006, Gehman et al. 2017).

If data and researchers from these efforts could be tracked through a centralized database, then in the event of an ecological emergency, such as the disease-driven declines discussed above, baseline samples could quickly be accessed and evaluated. Importantly, these resources would support the development of networks formed to address disease outbreaks (Groner et al. 2016). To enable a broader adoption of the practices described above, we propose a Web-based platform housing centralized information on parasitological databases (e.g., see Appendix S1: Table S1), collection techniques, and directories of researchers willing to participate in cross-disciplinary collaborations (Fig. 1B).

The establishment and growth of a community of potential cross-collaborators is essential for rapidly expanding the scope of parasite data and incorporation into ecological research. Further, the existence of a collaborative community of parasitologists and ecologists can help launch new initiatives to pair rigorous taxonomic training with novel molecular approaches, and to catalyze training of a new generation of scientists who are uniquely equipped to capitalize on available and forthcoming collections of parasites. By bringing together people and existing databases and resources, this platform would enhance access to the expertise, approaches, and data needed to facilitate inclusion of parasites into ecological research.

CONCLUSIONS

In the systems where they are best studied, parasites are known to play major roles in the dynamics and persistence of populations as well as the structure and stability of communities and ecosystems (e.g., Dobson and Hudson 1992, Hudson et al. 1992, Mouritsen and Poulin 2002, Lafferty et al. 2006, Kuris et al. 2008, Holdo et al. 2009, Ezenwa et al. 2010, Sutherland et al. 2016, Monello et al. 2017). In the future, parasites may mediate or determine responses to environmental change, across ecological scales. Further, increasing evidence suggests that parasites are themselves responsive to environmental changes and sensitive to co-extinctions (Farrell et al. 2015, Spencer and Zuk 2016, Cizauskas et al. 2017). Thus, timely attention to their influence is critical for accurately predicting future ecological states. In short, ecologists should collect infection data to improve ecological understanding.

ACKNOWLEDGMENTS

We thank the Odum School of Ecology community for fostering the spirit of collaboration that underlies this work. We thank Dr. Kim Mouritsen for sharing data. We are grateful to Dawn Satterfield, Roger Satterfield, and Dr. Andrea Graham for providing housing for working group meetings. D.A.S. was supported by the James Smithson Fellowship and the David and Joan Challinor Fellowship at the Smithsonian National Zoo. A-L.M.G. was supported by a National Science Foundation Postdoctoral Research Fellowship in Biology and a Tula Foundation fellowship. Publication costs were covered by S.A.B.'s funding from the Keck Science Department of Claremont McKenna, Pitzer, and Scripps Colleges. All authors declare no conflicts of interest.

LITERATURE CITED

- Anderson, R. M., and R. May. 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. *Journal of Animal Ecology* 47:219–247.
- Bi, K., T. Linderoth, D. Vanderpool, J. M. Good, R. Nielsen, and C. Moritz. 2013. Unlocking the vault: next-generation museum population genomics. *Molecular Ecology* 22:6018–6032.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Burt, J. M., M. T. Tinker, D. K. Okamoto, K. W. Demes, K. Holmes, and A. K. Salomon. 2018. Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. *Proceedings of the Royal Society B: Biological Sciences* 285:20180553–20180559.
- Carroll, E. L., M. W. Bruford, J. A. DeWoody, G. Leroy, A. Strand, L. Waits, and J. Wang. 2018. Genetic and genomic monitoring with minimally invasive sampling methods. *Evolutionary Applications* 11:1094–1119.
- Cerny-Chipman, E. B., J. M. Sullivan, and B. A. Menge. 2017. Whelk predators exhibit limited population responses and community effects following disease-driven declines of the keystone predator *Pisaster ochraceus*. *Marine Ecological Progress Series* 570:15–28.
- Cizauskas, C. A., C. J. Carlson, K. R. Burgio, C. F. Clements, E. R. Dougherty, N. C. Harris, and A. J. Phillips. 2017. Parasite vulnerability to climate change: an evidence-based functional trait approach. *Royal Society Open Science* 4:160535.
- Decaestecker, E., D. Verreydt, L. De Meester, and S. A. J. Declerck. 2015. Parasite and nutrient enrichment effects on *Daphnia* interspecific competition. *Ecology* 96:1421–1430.
- Dobson, A. P., and P. J. Hudson. 1992. Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *Journal of Animal Ecology* 61:487–498.
- Duszyński, D. 2010. Rodent parasite data for the Sevilleta National Wildlife Refuge, New Mexico (1990–1998). Long Term Ecological Research Network. <http://dx.doi.org/10.6073/pasta/b739d2c75e142f5742b7bfe74c97d5c1>
- Edeline, E., A. Groth, B. Cazelles, D. Claessen, I. J. Winfield, J. Ohlberger, L. A. Vøllestad, N. C. Stenseth, and M. Ghil. 2016. Pathogens trigger top-down climate forcing on ecosystem dynamics. *Oecologia* 181:519–532.
- Ezenwa, V. O., R. S. Etienne, G. Luikart, A. Beja Pereira, and A. E. Jolles. 2010. Hidden consequences of living in a wormy world: nematode-induced immune suppression facilitates tuberculosis invasion in African buffalo. *American Naturalist* 176:613–624.
- Farrell, M. J., P. R. Stephens, L. Berrang Ford, J. L. Gittleman, and T. J. Davies. 2015. The path to host extinction can lead to loss of generalist parasites. *Journal of Animal Ecology* 84:978–984.
- Franson, J. C., M. Friend, S. E. J. Gibbs, and M. A. Wild. 2015. Field manual of wildlife diseases: U.S. Geological Survey Techniques and Methods 15. Pages 1–114.

- Frick, W. F., T. L. Cheng, K. E. Langwig, J. R. Hoyt, A. F. Janicki, K. L. Parise, J. T. Foster, and A. M. Kilpatrick. 2017. Pathogen dynamics during invasion and establishment of white-nose syndrome explain mechanisms of host persistence. *Ecology* 98:624–631.
- Galbreath, K. E., et al. 2019. Building an integrated infrastructure for exploring biodiversity: field collections and archives of mammals and parasites. *Journal of Mammalogy* 341:514–536.
- Gehman, A.-L. M., J. H. Grabowski, A. R. Hughes, D. L. Kimbro, M. F. Piehler, and J. E. Byers. 2017. Predators, environment and host characteristics influence the probability of infection by an invasive castrating parasite. *Oecologia* 183:139–149.
- Gravem, S. A., and S. G. Morgan. 2017. Shifts in intertidal zonation and refuge use by prey after mass mortalities of two predators. *Ecology* 98:1006–1015.
- Groner, M. L., et al. 2016. Managing marine disease emergencies in an era of rapid change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150364.
- Harmon, A., D. T. J. Littlewood, and C. L. Wood. 2019. Parasites lost: using natural history collections to track disease change across deep time. *Frontiers in Ecology and the Environment* 17:157–166.
- Hewson, I., K. S. I. Bistolas, E. M. Quijano Cardé, J. B. Button, P. J. Foster, J. M. Flanzenbaum, J. Kocian, and C. K. Lewis. 2018. Investigating the complex association between viral ecology, environment, and northeast pacific sea star wasting. *Frontiers in Marine Science* 5:77.
- Hewson, I., et al. 2014. Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences* 111:17278–17283.
- Holdo, R. M., A. R. E. Sinclair, A. P. Dobson, K. L. Metzger, B. M. Bolker, M. E. Ritchie, and R. D. Holt. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biology* 7:e1000210–e1000212.
- Hudson, P. J., A. P. Dobson, and D. Newborn. 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. *Journal of Animal Ecology* 61:681–692.
- Hutchinson, G. 1961. The paradox of the plankton. *American Naturalist* 95:137–145.
- Jacquin, L., S. M. Reader, A. Boniface, J. Mateluna, I. Patalas, F. Pérez Jvostov, and A. P. Hendry. 2016. Parallel and nonparallel behavioural evolution in response to parasitism and predation in Trinidadian guppies. *Journal of Evolutionary Biology* 29:1406–1422.
- Justine, J.-L., M. J. Briand, and R. A. Bray. 2012. A quick and simple method, usable in the field, for collecting parasites in suitable condition for both morphological and molecular studies. *Parasitology Research* 111:341–351.
- Kay, S. W. C., A.-L. M. Gehman, and C. D. G. Harley. 2019. Reciprocal abundance shifts of the intertidal sea stars, *Evasterias troschelii* and *Pisaster ochraceus*, following sea star wasting disease. *Proceedings of the Royal Society B: Biological Sciences* 286:20182766–20182769.
- Kilpatrick, A. M., C. J. Briggs, and P. Daszak. 2010. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends in Ecology & Evolution* 25:109–118.
- Kock, R. A., et al. 2018. Saigas on the brink: multidisciplinary analysis of the factors influencing mass mortality events. *Science Advances*. <http://dx.doi.org/10.1126/sciadv.aao2314>
- Kuris, A. M., R. F. Hechinger, J. Shaw, K. Whitney, L. Aguirre-Macedo, C. Boch, A. P. Dobson, E. Dunham, B. Fredensborg, and T. Huspeni. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454:515–518.
- Lafferty, K. D., A. P. Dobson, and A. M. Kuris. 2006. Parasites dominate food web links. *Proceedings of the National Academy of Sciences* 103:11211–11216.
- Larsen, M., and K. N. Mouritsen. 2009. Increasing temperature counteracts the impact of parasitism on periwinkle consumption. *Marine Ecological Progress Series* 383:141–149.
- Lavery, C., D. Brenner, C. McIlwaine, J. J. Lennon, J. T. A. Dick, F. E. Lucy, and K. A. Christian. 2017. Temperature rise and parasitic infection interact to increase the impact of an invasive species. *International Journal for Parasitology (United Kingdom)* 47:291–296.
- Leboeuf, A. 2011. Making Sense of One Health: Cooperating at the Human-Animal- Ecosystem Health Interface. <https://www.ifri.org/en/publications/enotes/notes-de-lifri/making-sense-one-health>
- Lloyd, M. M., and M. H. Pespeni. 2018. Microbiome shifts with onset and progression of sea star wasting disease revealed through time course sampling. *Scientific Reports* 8:16476.
- Menge, B. A., E. B. Cerny-Chipman, A. Johnson, J. Sullivan, S. Gravem, and F. Chan. 2016. Sea star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: insights into differential population impacts, recovery, predation rate, and temperature effects from long-term research. *PLoS ONE* 11:e0153994.

- Mertens, N. L., B. D. Russell, and S. D. Connell. 2015. Escaping herbivory: ocean warming as a refuge for primary producers where consumer metabolism and consumption cannot pursue. *Oecologia* 179:1223–1229.
- Miner, M. C., et al. 2018. Large-scale impacts of sea star wasting disease (SSWD) on intertidal sea stars and implications for recovery. *PLoS ONE* 13:e0192870.
- Monello, R. J., N. L. Galloway, J. G. Powers, S. A. Madsen-Bouterse, W. H. Edwards, M. E. Wood, K. I. O'Rourke, and M. A. Wild. 2017. Pathogen-mediated selection in free-ranging elk populations infected by chronic wasting disease. *Proceedings of the National Academy of Sciences of the United States of America* 114:12208–12212.
- Montecino-Latorre, D., M. E. Eisenlord, M. Turner, R. Yoshioka, C. D. Harvell, C. V. Pattengill-Semmens, J. D. Nichols, and J. K. Gaydos. 2016. Devastating transboundary impacts of sea star wasting disease on subtidal asteroids. *PLoS ONE* 11:e0163190.
- Moritsch, M. M., and P. T. Raimondi. 2018. Reduction and recovery of keystone predation pressure after disease-related mass mortality. *Ecology and Evolution* 8:3952–3964.
- Mouritsen, K. N., and R. Poulin. 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* 124:101–117.
- Schultz, J. A., R. N. Cloutier, and I. M. Côté. 2016. Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ* 4:e1980.
- Schurer, J. M., E. Mosites, C. Li, S. Meschke, and P. Rabinowitz. 2016. Community-based surveillance of zoonotic parasites in a “One Health” world: a systematic review. *One Health* 2:166–174.
- Seebens, H., et al. 2017. No saturation in the accumulation of alien species worldwide. *Scientific Reports* 8:1–9.
- Selakovic, S., P. C. de Ruiter, and H. Heesterbeek. 2014. Infectious disease agents mediate interaction in food webs and ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 281:20132709.
- Sengupta, M. E., et al. 2019. Environmental DNA for improved detection and environmental surveillance of schistosomiasis. *Proceedings of the National Academy of Sciences of the United States of America* 116:8931–8940.
- Spencer, H. G., and M. Zuk. 2016. For host's sake: the pluses of parasite preservation. *Trends in Ecology & Evolution* 31:341–343.
- Springer, Y. P., et al. 2016. Tick-, mosquito-, and rodent-borne parasite sampling designs for the national ecological observatory network. *Ecosphere* 7:e01271.
- Sutherland, K. P., B. Berry, A. Park, D. W. Kemp, K. M. Kemp, E. K. Lipp, and J. W. Porter. 2016. Shifting white pox aetiologies affecting *Acropora palmata* in the Florida Keys, 1994–2014. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150205–20150217.
- Tobler, M., M. Plath, H. Burmeister, and I. Schlupp. 2006. Black spots and female association preferences in a sexual/asexual mating complex (Poecilia, Poeciliidae, Teleostei). *Behavioral Ecology and Sociobiology* 60:159–165.
- Tompkins, D. M., A. M. Dunn, M. J. Smith, and S. Telfer. 2011. Wildlife diseases: from individuals to ecosystems. *Journal of Animal Ecology* 80:19–38.
- Tompkins, D. M., A. W. Sainsbury, P. Nettleton, D. Buxton, and J. Gurnell. 2002. Parapoxvirus causes a deleterious disease in red squirrels associated with UK population declines. *Proceedings of the Royal Society B: Biological Sciences* 269:529–533.
- Torres, P. J., and S. T. Kelley. 2017. Sampling, extraction, and high-throughput sequencing methods for environmental microbial and viral communities. Pages 163–173 in S. R. Head, P. Ordoukhanian, and D. R. Salomon, editors. *Next generation sequencing*. Humana Press, New York, New York, USA.
- Wood, C. L., J. E. Byers, K. L. Cottingham, I. Altman, M. J. Donahue, and A. M. H. Blakeslee. 2007. Parasites alter community structure. *Proceedings of the National Academy of Sciences of the United States of America* 104:9335–9339.
- Wood, C. L., and P. T. J. Johnson. 2015. A world without parasites: exploring the hidden ecology of infection. *Frontiers in Ecology and the Environment* 13:425–434.
- Yeates, D. K., A. Zwick, and A. S. Mikheyev. 2016. ScienceDirect Museums are biobanks: unlocking the genetic potential of the three billion specimens in the world's biological collections. *Current Opinion in Insect Science* 18:83–88.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2770/full>