Beyond the tangled bank: An evolving meta-ecosystems framework to integrate ecological and evolutionary perspectives

Brandon M. Lind[1,2*], Ian N. C. Shuman[3,4],
Linda A. Deegan[5], Mary Heskel[6], Mark C. Urban[1,7], Jill L. Wegrzyn[1,2], and Peter A.H. Westley[8]

[1]Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA
[2]Institute for Systems Genomics, University of Connecticut, Storrs, CT 06269, USA
[3]Department of Earth and Environmental Sciences, Columbia University, New York, NY 10027, USA
[4]Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA
[5]Woodwell Climate Research Center, Falmouth, MA 02540, USA
[6]Department of Biology, Macalester College, Saint Paul, MN 55105, USA
[7]Center of Biological Risk, University of Connecticut, Storrs, CT 06269, USA.
[8]College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA

26 March 2026

Running title: Beyond the tangled bank
Keywords: evolution, meta-ecosystems, eco-evolutionary dynamics, ecosystem coupling

*Corresponding Author

Brandon M. Lind
ORCID: 0000-0002-8560-5417
Email: lind.brandon.m@gmail.com

Ian N. C. Shuman
ORCID: 0009-0008-2581-6037

Linda A. Deegan
ORCID: 0000-0002-1017-9599

Mary Heskel
ORCID: 0000-0003-3227-2978

Mark C. Urban
ORCID: 0000-0003-3962-4091

Jill L. Wegrzyn
ORCID: 0000-0001-5923-0888

Peter A.H. Westley
ORCID: 0000-0003-4190-7314

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us."

Charles Darwin, *On the Origin of Species*

Darwin's tangled bank (Darwin 1859) describes life as a network of interdependent organisms shaped by what we now think of as eco-evolutionary processes. This metaphor has gained renewed relevance in the 21st century, as rapid environmental and land-use changes drive ecological reorganization at multiple biological and spatial scales. Yet Darwin's metaphor was largely local – a single bank. While species interactions and selection pressures can take place at relatively local spatial scales, energy, resources, and organisms move across atmospheric, terrestrial, and aquatic boundaries, connecting ecosystems into large-scale, meta-ecosystem networks (Loreau et al. 2003). The meta-ecosystem framework combines concepts from meta-population and metacommunity theory – which describe spatially structured populations of one or more species connected by the flow of individuals and their interactions – with those from ecosystem ecology – through the tracking of the sources, sinks, and fluxes of energy and materials. Together, it describes dynamics of multiple ecosystems connected by the flows of energy, materials, and organisms across ecosystem boundaries. This conceptual foundation has provided a powerful framework to understand emergent properties of these networks that arise from spatiotemporal coupling within and across constituent components (Massol et al. 2011). Subsequent empirical studies have found that fluxes across system boundaries can fundamentally change community structure, population dynamics, and ecosystem properties and functions (Gounand et al. 2018). Yet, despite its strengths, meta-ecosystem theory has remained predominantly focused on ecological dynamics, largely ignoring intraspecific genetic variation that provides the substrate for evolution by natural selection. Therefore, the very processes implicit in Darwin's *On the Origin of Species* and his tangled bank metaphor are rarely considered within the meta-ecosystem framework.

The relevance of evolution to meta-ecosystem dynamics

Over the last several decades, there has been increasing recognition that adaptive evolution can take place over a few generations, on similar timescales as ecological change, and over fine, microgeographic scales (Carroll et al. 2007; Richardson et al. 2014). Furthermore, the traits that respond to natural selection – such as phenology, growth, stress tolerance, resource allocation, and reproduction – can influence ecosystem processes, such as productivity, decomposition, carbon sequestration, and even landscape morphology and geophysical properties (Dong et al. 2024). Yet despite the exclusion of evolutionary dynamics within theoretical meta-ecosystem models, there is ample evidence that evolutionary change can cause ecological change across ecosystem boundaries. For example, black cottonwood (*Populus trichocarpa*) grows in riparian zones and delivers annual pulses of leaf litter into streams and rivers, providing a major subsidy that supports aquatic food webs. Common gardens have shown that genetic variation in leaf senescence (i.e., phenology) alters decomposition rates and aquatic invertebrate richness (Rodriguez-Cabal et al. 2017). Further, studies in other *Populus* species have shown that genetic variation in leaf chemistry also influences decomposition, invertebrate assemblages, and soil net nitrogen (Schweitzer et al. 2008). These and other examples – such as recent body size declines in Pacific salmon and subsequent decreases in marine-derived nutrient transport to freshwater systems (Oke et al. 2020) – illustrate that variation and contemporary changes in key traits can alter meta-ecosystem dynamics through the flow of material, energy, and organisms across ecosystem boundaries.

The evolving meta-ecosystem framework

In the face of global change and the recognition of the potential for evolutionary influence on meta-ecosystem coupling, it is urgent to address: how does adaptive evolution shape mechanistic responses to climate change at multiple levels of biological organization – from genes to ecosystems – and determine the resilience of meta-ecosystem functions? To accurately address this question, meta-ecosystems cannot be treated simply as networks of habitats connected by flows, but instead as dynamic systems with connections that are mediated by organismal evolution and ecological feedbacks – an *evolving* meta-ecosystem (Figure 1).

We argue that a change in thinking is needed, where we seek to identify the mechanisms and relationships that would allow adaptive evolution to influence dynamics at the meta-ecosystem scale. Determining whether evolutionary responses to climate change have consequential impacts on spatiotemporal meta-ecosystem dynamics then requires testing for underlying relationships among: (1) the patterns and drivers of environmental change; (2) the evolution of heritable, genetically-based traits (including heritable plasticity) that – directly or indirectly – impact cross-boundary flows; (3) changes in the properties of these flows (e.g., the direction, magnitude, and spatiotemporal variation and synchrony); and (4) how these properties impact meta-ecosystem function and stability – for example, in carbon or nutrient balance, trophic subsidies, connectivity, feedback dynamics, or the resilience of coupled meta-ecosystem functions to disturbance or environmental change.

Experimental designs and the necessary data to understand evolving meta-ecosystem dynamics

To address these conditions, researchers should consider the types of data and experimental designs that are needed to quantify these dynamics across multiple biological and ecological levels of organization. Temporal and contemporary approaches offer complementary perspectives. For instance, retrospective or long-term observations and experiments can each be

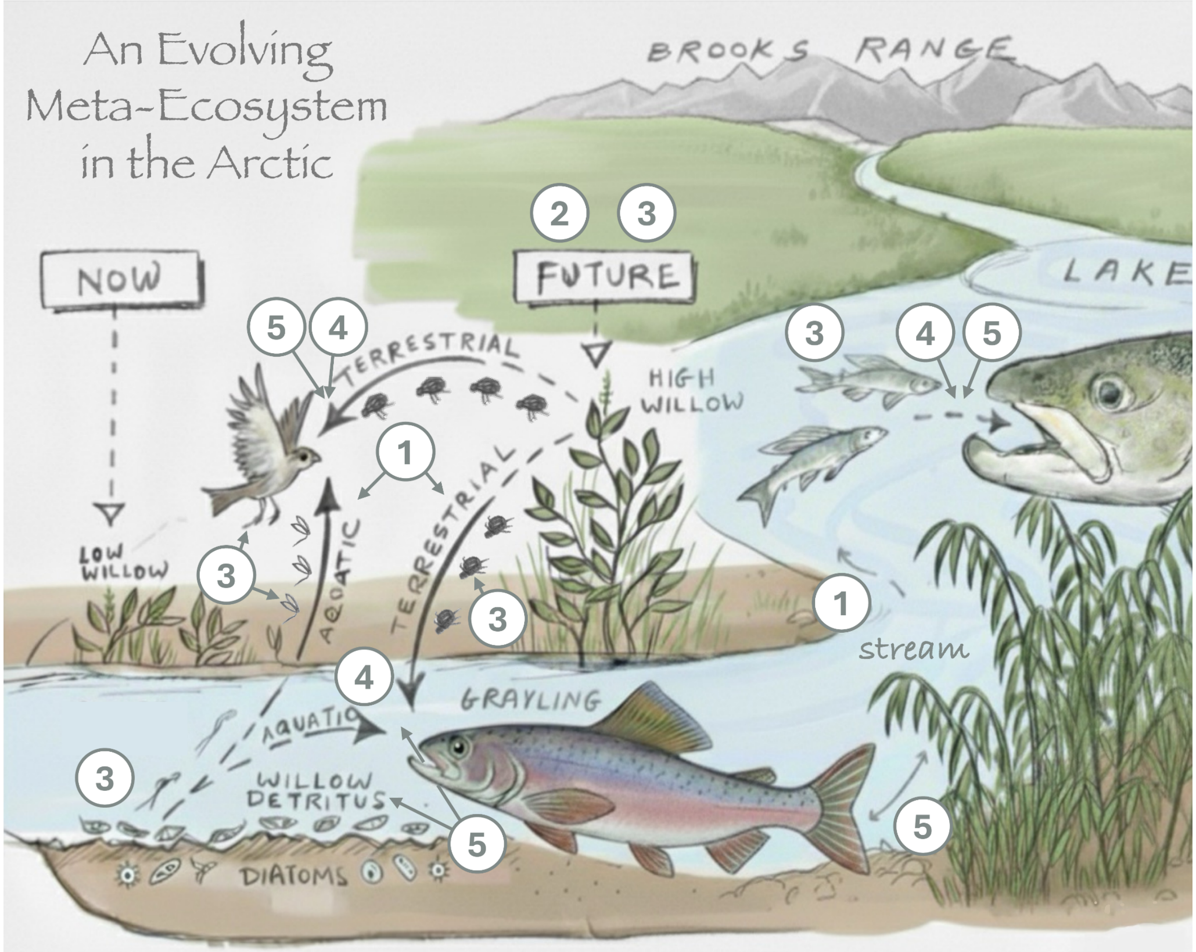

Figure 1 Evolutionary processes impact cross-boundary flows of energy, materials, and organisms in an evolving meta-ecosystem. This figure depicts a tangled bank within an Arctic stream-riparian meta-ecosystem network, where contemporary climate-driven evolution and expansion of a dominant willow species (*Salix alaxensis*) alters ecological and evolutionary dynamics within and across terrestrial and aquatic ecosystem boundaries. In this evolving meta-ecosystem, cross-boundary flows (1) – including willow leaf litter, emerging insects, and movement of Arctic grayling (*Thymallus arcticus*) and white-crowned sparrow (*Zonotrichia leucophrys*) – influence, interact with, and feedback into evolutionary responses of plant phenology and growth (2), population dynamics of insect, bird, and fish species (3), species interactions within and across ecosystem boundaries (4), and nutrient cycling regimes (5). Likewise, each of these aspects can influence, interact with, and feedback into other properties within and across boundaries of the meta-ecosystem.

used to demonstrate evolutionary change. Moreover, evidence of quantitative evolutionary change that coincides with environmental change can provide evidence for an adaptive response. Resurrection studies of seeds collected from natural or human-mediated seed banks, for example, can reveal how ecologically relevant traits have shifted over periods of changing temperature, hydrology, or nutrient regimes (Christie et al. 2023). Herbarium and museum collections can also provide material for time-series genomics data, which can be used to quantify signals of adaptive responses at the genetic level. Similarly, long-term ecological research and monitoring networks can capture both ecological and evolutionary change (Cocciardi et al. 2024).

Contemporary organismal approaches complement these temporal perspectives. Common gardens or transplant experiments (both long- and short-term) along ecological gradients can quantify the heritable and environmental components of phenotypic variation – including genetic correlations (e.g., trade-offs) – for traits that underlie fitness, mediate meta-ecosystem flows, or both (Blum et al. 2021). These experiments can also disentangle heritable plasticity from non-heritable plasticity, an important factor to consider for species persistence (Ashander et al. 2016). Additionally, population genomic tools – such as genome-wide association studies and scans for selective sweeps – as well as landscape genomic perspectives – which can estimate demographic histories, quantify spatial genetic structure, and relationships between environmental and genetic variation – can identify the genetic components underlying these traits while estimating the strength, timing, and spatial pattern of selection and evolution (Bernatchez et al. 2023). Similarly, comparative genomics can reveal patterns of gene family evolution, structural variation, and selective signals that may underlie adaptive strategies within lineages.

These temporal and contemporary methods quantifying organismal evolution, alongside ecosystem-level measurements or experimental manipulations – on properties such as nutrient supply and stoichiometry, productivity, matter transport rates, dissolved gases, hydrologic discharge, organismal emergence rates, movement, and migration, or trophic subsidy fluxes – allow for explicit analyses of whether genetically based trait variation alters cross-ecosystem fluxes. Additionally, these complementary datasets can also reveal when trait evolution amplifies, dampens, creates, synchronizes, disrupts, or reorganizes spatial flows among meta-ecosystems (Urban et al. 2020), and thus how trait evolution affects meta-ecosystem stability.

The Arctic as a tractable system to observe evolving meta-ecosystem dynamics

Ecosystems characterized by relatively low species diversity and strong, well-defined coupling between ecosystems present tractable settings for developing the evolving meta-ecosystem framework. Identifying focal study organisms is critical, but even within simplified ecosystems, this can be difficult. Thus, dominant or foundation species – including those that occupy or move across ecosystem boundaries – that mediate the abundance and flow of energy, material, and organisms offer a practical starting point (Whitham et al. 2003). Systems experiencing ongoing and rapid environmental change offer further opportunities to observe relationships between evolution and evolving meta-ecosystem dynamics.

The Arctic is well-suited for observing and understanding such dynamics. For example, the rate of Arctic warming is four times faster than global averages (Rantanen et al. 2022), leading to spatially structured selective pressures and large-scale shifts in vegetation, permafrost, hydrology, and biogeochemical cycles (Frost et al. 2025) that provide opportunities to observe evolutionary and ecological change in real time. The Arctic has a history of extensive long-term ecological research and observatory networks that provide the temporal and spatial resolution necessary to investigate multi-level dynamics. The Arctic's tundra and stream-riparian meta-ecosystems are each connected by strong coupling between biotic and abiotic processes and are composed of a few key species that have disproportionately large ecosystem impacts, where even subtle shifts in community or functional composition can trigger cascading effects at the ecosystem level (Wookey et al. 2009). The expansion of tall deciduous shrubs along stream networks is one of the clearest biological signals of Arctic warming (Myers-Smith et al. 2020) and underscores the potential for rapid change to affect multiple dimensions of meta-ecosystem coupling.

As a dominant species at the boundaries of stream-riparian zones, evolutionary change resulting in the expansion and increased growth of the widespread riparian feltleaf willow (*Salix alaxensis*) can have substantial cross-system impacts (Figure 1). For example, taller, denser Arctic willows increase habitat and resources for both terrestrial insects and birds (Boelman et al. 2014) and influence levels of organic matter entering streams. Impacts to aquatic and terrestrial insect abundance may in turn affect trophic subsidies for freshwater fish such as Arctic grayling (*Thymallus arcticus*) and migratory birds such as white-crowned sparrows (*Zonotrichia leucophrys*), potentially altering the flow of energy, materials, and organisms between terrestrial and aquatic ecosystems. By revealing how evolutionary changes in dominant species can cascade across meta-ecosystem boundaries – affecting temperature regimes, nutrient fluxes, organismal abundance and diversity – Arctic stream-riparian networks provide a tractable model with principles that extend beyond polar environments, offering a translational framework for studying evolving meta-ecosystem dynamics.

Summary

Darwin's tangled bank describes a local network of interconnected organisms resulting from ecological and evolutionary processes. An evolving meta-ecosystem perspective extends that metaphor to spatially dynamic interactions with consequences and feedbacks at the landscape scale, mediated by evolutionary and ecological dynamics in real time. This integrative and cross-disciplinary framework therefore offers a generalizable approach to studying eco-evolutionary dynamics in a rapidly changing world.

Author Contributions

B.M.L. drafted and revised the manuscript with input and assistance from I.N.C.S., L.A.D., M.H., C.N., M.C.U., J.L.W., and P.A.H.W. Authors L.A.D., M.H., C.N., M.C.U., J.L.W., and P.A.H.W. led the conceptualization of the EVOME framework and funding acquisition.

Acknowledgements

The authors are supported by the Evolving Meta-Ecosystems (EVOME) Biology Integration Institute (NSF BII 2320675). The authors would like to thank Robert Golder for the basis of the sketch used for Figure 1.

ORCID

Brandon M. Lind http://orcid.org/0000-0002-8560-5417

Ian N. C. Shuman http://orcid.org/0009-0008-2581-6037

Linda A. Deegan http://orcid.org/0000-0002-1017-9599

Mary Heskel http://orcid.org/0000-0003-3227-2978

Christopher Neill http://orcid.org/0000-0002-0232-8371

Mark C. Urban http://orcid.org/0000-0003-3962-4091

Jill L. Wegrzyn http://orcid.org/0000-0001-5923-0888

Peter A.H. Westley http://orcid.org/0000-0003-4190-7314

References

Ashander, J., L.-M. Chevin, and M. L. Baskett. 2016. Predicting evolutionary rescue via evolving plasticity in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences* 283: 20161690.

Bernatchez, L., A.-L. Ferchaud, C. S. Berger, C. J. Venney, and A. Xuereb. 2023. Genomics for monitoring and understanding species responses to global climate change. *Nature Reviews Genetics*: 1–19.

Blum, M. J., C. J. Saunders, J. S. McLachlan, J. Summers, C. Craft, and J. D. Herrick. 2021. A century-long record of plant evolution reconstructed from a coastal marsh seed bank. *Evolution Letters* 5: 422–431.

Boelman, N. T., L. Gough, J. Wingfield, S. Goetz, A. Asmus, H. E. Chmura, J. S. Krause, et al. 2015. Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biology* 21: 1508–1520.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. *Functional Ecology* 21: 387–393.

Christie, K., N. R. Pierson, L. M. Holeski, and D. B. Lowry. 2023. Resurrected seeds from herbarium specimens reveal rapid evolution of drought resistance in a selfing annual. *American Journal of Botany* 110: e16265.

Cocciardi, J. M., A. M. Hoffman, D. F. Alvarado-Serrano, J. Anderson, M. Blumstein, E. L. Boehm, L. G. Bolin, et al. 2024. The value of long-term ecological research for evolutionary insights. *Nature Ecology & Evolution* 8: 1584–1592.

Darwin, C. 1859. On the origin of species.

Dong, X., M. F. Stokes, A. P. Hendry, L. G. Larsen, and G. A. Dolby. 2024. Geo-evolutionary feedbacks: integrating rapid evolution and landscape change. *Trends in Ecology & Evolution* 39: 863–876.

Gounand, I., E. Harvey, C. J. Little, and F. Altermatt. 2018. Meta-Ecosystems 2.0: Rooting the Theory into the Field. *Trends in Ecology & Evolution* 33: 36–46.

Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6: 673–679.

Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters* 14: 313–323.

Oke, K. B., C. J. Cunningham, P. A. H. Westley, M. L. Baskett, S. M. Carlson, J. Clark, A. P. Hendry, et al. 2020. Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications* 11: 4155.

Rantanen, M., A. Yu. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma, and A. Laaksonen. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*3: 168.

Richardson, J. L., M. C. Urban, D. I. Bolnick, and D. K. Skelly. 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology & Evolution* 29: 165–176.

Rodriguez-Cabal, M. A., M. N. Barrios-Garcia, S. M. Rudman, A. D. McKown, T. Sato, and G. M. Crutsinger. 2017. It is about time: genetic variation in the timing of leaf-litter inputs influences aquatic ecosystems. *Freshwater Biology* 62: 356–365.

Schweitzer, J. A., M. D. Madritch, J. K. Bailey, C. J. LeRoy, D. G. Fischer, B. J. Rehill, R. L. Lindroth, et al. 2008. From Genes to Ecosystems: The Genetic Basis of Condensed Tannins and Their Role in Nutrient Regulation in a Populus Model System. *Ecosystems* 11: 1005–1020.

Urban, M. C., S. Y. Strauss, F. Pelletier, E. P. Palkovacs, M. A. Leibold, A. P. Hendry, L. D. Meester, et al. 2020. Evolutionary origins for ecological patterns in space. *Proceedings of the National Academy of Sciences* 117: 17482–17490.

Whitham, T. G., W. P. Young, G. D. Martinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, G. M. Wimp, et al. 2003. Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology* 84: 559–573.

Wookey, P. A., R. Aerts, R. D. Bardgett, F. Baptist, K. A. Bråthen, J. H. C. Cornelissen, L. Gough, et al. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology* 15: 1153–1172.