

## OVERVIEW

Human-driven climate change now alters and rearranges biological systems at unprecedented rates. These changes play out across large and connected landscapes, or meta-ecosystems, in which many important connections are the movements, interactions, and evolution of organisms. The mechanisms that drive these rearrangements occur across scales from genes to meta-ecosystems in landscapes. New evidence that evolution can occur rapidly necessitates a major reappraisal of the longstanding paradigm that meta-ecosystem dynamics, in the face of rapid climate or other changes over even short time spans, can be understood without evolution. Yet biological science today is ill-prepared to address this complexity because most biologists work within subsets of these scales and disciplines.

This project will create an **Evolving Meta-Ecosystems Institute (EvoME)** that connects biologists through research and education across the scales of genes to meta-ecosystems. EvoME will create research and training opportunities focused on how multiple levels of biological organization interact to shape changes in connected river and tundra meta-ecosystems of the Alaskan Arctic. The Arctic is one of the most rapidly warming places on Earth, but one in which a tractable number of species in river and adjacent tundra ecosystems will allow quantification of the genes, traits, physiology, movements, adaptation and evolution of major species, and the flows of energy, nutrients and organisms. It will partner geneticists, evolutionary biologists, physiologists, population biologists, community ecologists, ecosystem ecologists, quantitative biologists, and modelers. It will create structured interactions among scientists, students, and journalists to promote integrated biological research, and train a next generation of diverse and integrative biologists. EvoME will increase public understanding of the importance and implications of highly integrated biological science to understand large-scale responses to climate change.

## INTELLECTUAL MERIT

Understanding how biological systems interact over space and time is a Grand Challenge for biology. Limited integration across biological disciplines has impeded advances. Studies are needed to connect the genes that determine individual performance to the functioning of Earth's ecosystems and their spatial connections in meta-ecosystems across landscapes. EvoME will address core questions in genomics, molecular genetics, physiology, evolution, ecology, and ecosystem biology and *unite* these disciplines to create new integrated understanding that extends to meta-ecosystems and considers potentially rapid evolutionary responses to a warming world. The proposal advances theory and understanding by: (1) challenging the existing paradigm that predictions about climate change responses can ignore genetics and adaptive evolution; (2) integrating from genes to meta-ecosystems to understand how each biological level interacts with the others; (3) testing the many pathways through which animal behavioral and foodweb responses can interact with evolution; (4) using powerful genomic data to quantify the genes underlying trait and ecosystem responses; and (5) leveraging novel bio-monitoring equipment, computational algorithms, and new modeling techniques to develop flexible and adaptable forecasting tools. In these ways, EvoME will contribute to a broader, more mechanistic and predictive understanding of ecological and evolutionary responses of Earth's meta-ecosystems to climate change.

## BROADER IMPACTS

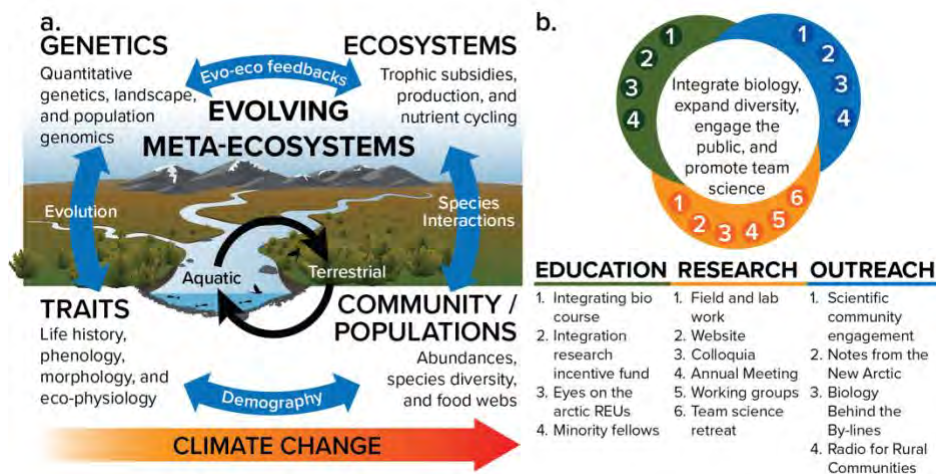
The EvoME Institute will benefit society by creating the next generation of biologists trained to think across disciplines, improving science communication, and enhancing diversity—including Native Alaskans—in STEM fields. It will expand opportunities for undergraduate and graduate study, promote minority recruitment and retention, and create structured opportunities for cross-disciplinary research by bringing together diverse teams of faculty and students. EvoME will broaden scientific literacy for the public by partnering researchers, students, and journalists both in the field in Alaska and in a cutting-edge genomics laboratory. Products of these interactions will include communication with the public via blogs, social media, and radio stories that will be broadcast to remote local communities including Native Alaskans.

## 1. RATIONALE, JUSTIFICATION AND INTEGRATION OF THE RESEARCH THEME

*The overarching theme of the EVOLVING META-ECOSYSTEMS INSTITUTE is to understand how adaptive evolution shapes mechanistic responses to climate change at multiple levels of biological organization from genes to ecosystems, and determines the resilience of meta-ecosystem functions.*

**OVERVIEW:** EvoME (/ē vōm/), the **Evolving Meta-Ecosystems Institute**, provides an exceptional opportunity for integrating across biological disciplines and scales of organization to understand how and to what degree adaptive evolution can maintain and shape meta-ecosystem function – the combined function of individual ecosystems that are linked by the flow of evolving organisms and energy – in response to climate change (Fig. 1a). Spatial flows are ubiquitous in nature and induce mutual feedbacks among different ecosystems, thus the meta-ecosystem perspective is needed to understand the dynamics of ecosystems and their responses to climate change. Studying the biology of organisms in their natural habitat is important because it provides a more complete view of biological processes and a better capacity to understand and predict the natural world. Although the goals of EvoME could be addressed in any ecosystem, EvoME will focus on the stream-riparian meta-ecosystem within the Arctic biome because its inherently small and tractable number of dominant species, our combined experience and significant long-term research

efforts that can be leveraged, and the fact that the Arctic is warming 4x faster than anywhere else on Earth. In turn, the understanding gained from studying meta-ecosystems of the Arctic will yield insight into how meta-ecosystems from other biomes will respond to climate change.



**Fig. 1. Conceptual Diagram.** (a) Vision for an Evolving Meta-Ecosystems Institute that connects genomics, traits, communities and populations, and ecosystems to the functioning of linked aquatic-terrestrial meta-ecosystems in a warming Arctic. (b) Integrating activities that span research, education, and outreach.

### INTEGRATION

Our vision for EvoME (Fig. 1a) synthesizes understanding of the spatial variability of natural selection and the genetic basis of organismal traits, demography at the population level, and species interactions at the community level to determine their influence on ecosystem and meta-ecosystem dynamics. This information is integrated into a trait-based model to understand current and predict future meta-ecosystem functions. Our work connects state-of-the-art research in: (1) bioinformatics, (2) biogeochemistry, (3) animal behavior, (4) ecosystem ecology, (5) evolutionary biology, (6) genetics and genomics (including quantitative genetics and population and landscape genomics), (7) physiology, (8) population and community ecology, and (9) quantitative biology. Complementary disciplines include Earth science, communications, and team science.

We will achieve biological integration through a commitment to a shared research theme that depends on deep understanding in specialties in biology and full interdependency with other biological fields, deliberate mentoring in team science that builds interactions and communication across disciplines, and education and outreach intertwined with the research. We include multiple mechanisms (Fig. 1b) that foster integration of biological disciplines including: concentration of interactive field work focused in a

single location with parallel measures on multiple organisms, an online program management dashboard, academic year colloquia that feature speakers of different disciplines and underrepresented groups who then have the opportunity to become EvoME Fellows with funds for research, in-person annual meetings (with remote option) that rotate among institutions, cross-cutting working groups with early-career scientists in leadership positions, hosting of national symposia, and annual *Team Science Retreats*. Integrating Education and Outreach activities include a team-taught *Integrating Biology* course, a research integration fund for graduate students that requires participation by students in multiple disciplines, a co-mentoring *Biology Behind the By-lines* program between scientists and journalists, an REU program in which students spend time in the Arctic and in labs, student and postdoc training in science communication in collaboration with journalists, and production of blog and radio pieces for both rural Arctic and more general public audiences.

## **RATIONALE**

The discovery that evolutionary adaptation can occur within a few generations and at spatial scales that alter contemporary ecological dynamics<sup>16-26</sup> compels a paradigmatic shift in ecosystem science towards one that recognizes the role of adaptive evolution on meta-ecosystem function. Despite a few exemplary studies<sup>27-29</sup>, literature reviews have uncovered few studies that trace evolutionary change through to ecosystem change in nature<sup>25,30-32</sup>. This gap has arisen in part because evolutionary biologists have primarily focused on genetics, traits, and populations<sup>25,26,33-36</sup>, whereas ecosystem ecologists have typically focused on physical and biogeochemical processes. Integrating these two traditionally disconnected disciplines of biology by bridging intervening levels of biological organization is needed to understand if and to what degree adaptive evolution can influence the response of meta-ecosystems to any perturbation, but most especially climate change in our Arctic system<sup>28,29,31-33,37,38</sup>.

Trophic subsidies represent flows of energy, nutrients, and organisms that can span a wide range of spatial scales, occurring both within single ecosystems (e.g., within a forest stand or lake) and among ecosystems (e.g., between a forest stand, an adjacent open meadow, and a nearby water body)<sup>39-42</sup>. Trophic subsidies integrate across biological disciplines because spatiotemporal dynamics in the quality and quantity of trophic subsidies are determined by the genetic and biological traits of their component organisms, populations, and communities. Trophic subsidies usually flow from high- to low-production areas, and thus homogenizing the spatial variability of landscape production. For example, salmon migrating from oceans to inland ecosystems bring nitrogen and phosphorus that stimulate river and riparian productivity<sup>43,44</sup>. The magnitude of this trophic subsidy is determined by specific traits, such as body size<sup>45,46</sup>, that are also under selection from natural (climate change) and human (fishing) pressures.

Evolution could decrease or increase trophic subsidies, but the predominant pattern that we have found in the literature is that evolution usually dampens landscape heterogeneity and thus will likely reinforce organism-mediated trophic subsidies that re-distribute energy across the landscape<sup>27,37,47</sup>. A mechanistic and multi-scale understanding of how climate change will affect trophic dynamics is needed to identify and characterize differences in the direction and magnitude of adaptive responses among both organisms that differ across key traits like age span and dispersal (e.g., grayling vs. insects) and ecosystems (e.g., aquatic vs. terrestrial), and how those responses combine to influence meta-ecosystem functions.

Our research will focus on the stream-riparian meta-ecosystem in the Arctic but will be generalizable to meta-ecosystems in other biomes. That is because trophic subsidies occur in all biomes<sup>48-58</sup>, where they link ecosystems into integrated meta-ecosystems. Thus, the foundations developed here will have broad applicability. We will also develop trait-based models to connect performance-related traits of organisms to individual and population level distribution and success<sup>59-61</sup> that can also be applied elsewhere to forecast ecological outcomes in response to climate change<sup>62</sup>. The insights derived from assays of genetic and trait diversity within and across species will answer fundamental questions in the fields of genomics, physiology, evolution, ecology, and conservation of the Earth's biota.

## RESEARCH PROJECTS

EvoME will be organized around four integrated projects, each of which involves research that bridges biological disciplines and levels organization, links aquatic and terrestrial ecosystems, and requires integration of field observations and field and laboratory experiments into quantitative analyses and trait-based modeling.

In **Project 1**, we will measure **Ecological Dynamics** by assessing population abundances, full community compositions, productivity differences at multiple trophic levels, and reciprocal trophic subsidies between streams and terrestrial riparian meta-ecosystems across thermal-connectivity regions. We will conduct ecosystem experiments that test the impacts of change in trophic subsidies on ecosystem functions. In **Project 2, Landscape Variation in Traits and Genetics**, we will measure trait (phenotypic) and genomic (genotypic) variation across regions for the dominant organisms in stream-riparian meta-ecosystems – willow, mayfly, ground-beetle, Arctic grayling, and white-crowned sparrow – to understand how this variation correlates with ecosystem processes measured in *Project 1*. In **Project 3, Adaptive Responses to Future Climate Change**, we will build on the observed spatial variation in phenotypes and genotypes from *Project 2* to develop transplant and common garden experiments between contrasting environments to understand local adaptation and phenotypic plasticity in thermal response curves for key traits and to estimate selection and heritability in order to understand the role of plasticity, genetics, and their interaction in species responses to climate change. In **Project 4, Evolving Meta-Ecosystems**, we will synthesize results and insights from *Projects 1–3* to predict meta-ecosystem dynamics under future scenarios of climate change using newly developed Models of Evolving Meta-Ecosystems (MEMEs) based on traits, determined by both plasticity and genetics, and ecological interactions. We will validate these models by leveraging extensive datasets from the Long-term Ecological Research and National Ecological Observatory Networks, EvoME data, and our Meta-ecosystem Observing Network.

## EDUCATION, DIVERSITY, AND OUTREACH

**EDUCATION.** EvoME will develop: (1) a novel cross-institutional, interdisciplinary *Integrating Biology* course that enables students to understand both the depth of individual disciplines and how to integrate across multiple levels of biological organization; (2) an *Integration Incentive Fund* that will financially support discipline-spanning projects developed by student teams who partner with journalists to develop “pitch videos”; (3) an *Eyes on the Arctic* REU research immersion program; and (4) a *Team Science Retreat* held annually to improve collaboration and inclusion.

**DIVERSITY.** To promote a diverse research community, we will: (1) *increase retention* by mentoring individuals continuously from undergraduate (REU) through post-graduate careers; (2) expand our *scientist diversity* by providing seed funding and fellowships to scientists from underrepresented groups; (3) focus on fostering diversity, equity, and inclusion in *Team Science Retreats*; and (4) recruit in person at institutions and national meetings serving underrepresented groups.

**OUTREACH.** EvoME will use multiple points of intersection with research and education, and with science journalists, to educate participants to communicate integrated biology to broad audiences. A *Biology Behind the By-lines* Arctic immersion course will feature reciprocal mentoring of students and postdocs in communication by journalists, and mentoring of journalists by students in biology. Research stories developed in collaboration with journalists will feed into *Notes from the New Biology*, social media, a YouTube channel, and radio programs. Webcast EvoME *Colloquia* will target broader scientific audiences and the *Annual Meeting* will rotate among institutions.

**MANAGEMENT PLAN.** The Institute will be led by an Executive Committee that will make decisions by consensus and with input from an Advisory Board. Seven working groups (four around science themes and three around data integration, broader impacts, and team science) will be cross-linked by personnel and activities. Each WG will have members from all career stages and disciplines, and WG leaders will attend Executive Committee meetings quarterly. Annual *Team Science Retreats* and *Annual Meetings* will facilitate communication, integration, planning, and synthesis.

## 2. LIST OF PARTICIPANTS

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### **EXECUTIVE COMMITTEE**

**Linda A. Deegan** (PI; Scientist, Woodwell Climate Science Center) will direct the Center, lead the meta-ecosystem experiments, and mentor research assistants, post-docs, and students. **Mark Urban** (Co-PI; Prof., Ecology and Evolutionary Biology, UConn) will lead the thermal-connectivity gradient surveys, participate in common garden/transplant experiments and mentor students and postdocs. **Natalie Boelman** (Co-PI; Research Prof., Lamont-Doherty Earth Observatory, Columbia U.) will apply near/remote sensing, bioacoustics, and GPS animal tracking, collaborate on willow ecology, supervise PhD students and coordinate with the Arctic LTER. **Chris Neill** (Co-PI; Scientist, Woodwell) will conduct research on terrestrial nutrient cycling, lead the Broader Impacts WG and the journalist course, and mentor students. **Jill Wegrzyn** (Co-PI; Assoc. Prof. & Director, Computational Biology Core, Institute for Systems Genomics, UConn) will lead the Data WG, supervise genomic analysis, conduct the willow common garden/transplant experiments, and mentor PhD students and bioinformatics assistants. **Heidi Golden** (Research Associate, Woodwell) will be Institute Manager and lead the REU program.

### **INVESTIGATORS**

**Carla Atkinson** (Assoc. Prof., Biological Sciences, U. Alabama) will lead the Trait WG and conduct research on invertebrate stoichiometry, traits, common garden/transplant experiments, and mentor 2 PhD students. **Dan Bolnick** (Prof., Ecology and Evolutionary Biology, UConn) will share new tools in computer science and statistics to test for plastic and evolutionary changes in genetic and ecological networks. **Nigel Golden** (Postdoc, Woodwell) will be the first underrepresented minority EvoME Fellow who will conduct research and participate in recruitment of underrepresented minority students. **Donie Bret-Harte** (U Alaska Fairbanks, Toolik Field Station Science Director) brings her expertise as an Arctic plant ecologist and will facilitate activities at Toolik. **Mary Heskell** (Asst. Prof., Biology, Macalester College) will lead the Ecological WG research on willow ecology and co-supervise a Columbia U. PhD student. **Jeff Lozier** (Prof., Biological Sciences, University of Alabama) brings his expertise in whole genome sequencing to investigate adaptation, demography, and thermal tolerance of insects, share genomic computational techniques, and co-supervise 2 PhD students. **Anna Lilidahl** (Assoc. Scientist, Woodwell) will advise on Arctic hydrology and interface with her Permafrost Discovery Gateway and will share data and artificial intelligence approaches. **Sue Natali** (Scientist, Woodwell) will assist in diversity recruitment and retention through her Polaris Project and facilitate interactions with her Permafrost Pathways project. **Rachel O'Neill** (Prof. & Director, Institute for Systems Genomics and Center for Genome Innovation, UConn) will work on whole genome sequencing with the scientists who specialize in the ecology of the organism. **Cory Merow** (Asst. Research Prof., EEB, UConn) will lead the Meta-ecosystem WG, develop models integrating field observations and forecasting ecosystem function, and mentor students. **Peter Westley** (Assoc. Prof., Dept. of Fisheries, U. Alaska-Fairbanks-Fairbanks) will conduct Arctic grayling common garden experiments, lead the GXE (Genetics X Environment) WG, and mentor PhD students. **Erik Schoen** (Research Asst. Prof., Intl. Arctic Research Center, U. Alaska) will determine Arctic grayling traits and co-supervise PhD students. **Jesse Krause** (Asst. Prof., Bio., U Nevada-Reno) will advise on sparrow traits.

### **ADVISORY BOARD**

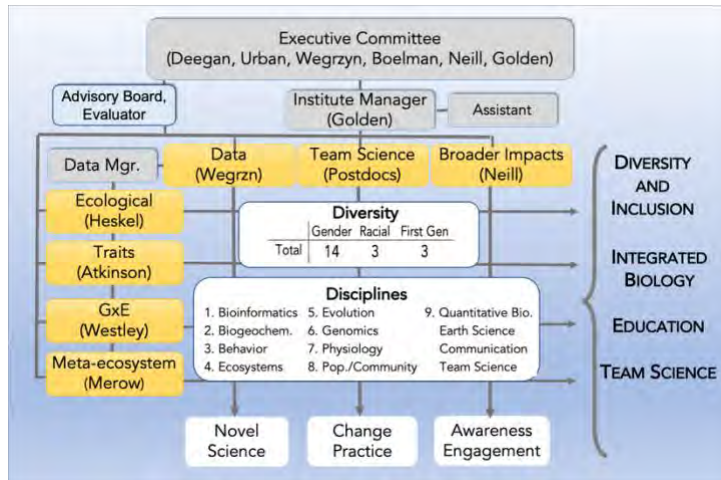
**John Wingfield** (U. California, Berkeley) will provide advice on interdisciplinary reach science. **Gillian Bowser** (U. Colorado, Natural Resource Ecology Lab) will bring her expertise in education and diversifying science. **Andrew Hendry** (McGill U., Dept. of Biology) will bring his internationally recognized expertise in eco-evolutionary dynamics.

### **TEAM SCIENCE, OUTREACH AND EVALUATION**

**Kathleen Weathers** (Scientist, Cary Inst.) will lead the *Team Science Retreat* focused on empowering diverse and early career scientists. **Christina Olex** (The Point) will lead *Team Science Retreat* discussions on team dynamics and equity. **Heather Goldstone** (Director of Communications, Woodwell) will lead the development of radio programs, co-lead the journalist course. **Arnell Garrett** (Delmarva Associates) will conduct formative and summative evaluations and assessments of the Institute.

### 3. PROJECT MANAGEMENT

**ORGANIZATION:** EvoME will consist of 21 investigators plus four experts in team science, communication, and evaluation at 14 institutions, as well as postdocs, research assistants, and graduate and undergraduate students. Each team member has primary expertise in one level of biology but also has experience and demonstrated commitment to connecting research and training students across levels of biology. The Institute will be organized around four research-oriented Working Groups (WGs) that have overlapping membership with three integrative WGs (Fig. 2). All WGs will have PIs, graduate students, postdocs, and scientists. All institute personnel will participate in at least two WGs.



**Fig. 2. Organization chart** of Leadership (gray), Working Groups (orange) and the Advisory Board and Evaluator (blue). Diversity and Inclusion, Integrated Biology, Education and Team Science underpin the Institute (entire box).

Deegan (PI) will serve as Institute Director. Overall management will lie with an **Executive Committee** that consists of Deegan, Urban, Wegrzyn, Boelman, Golden and Neill (Fig. 2). Working Group leads will be Merow, Westly, Atkinson, Heskel, Wegrzyn, Neill, and one rotating postdoc. The ExCom will meet monthly and operate by consensus. The Working Group leads, Data Manager, and Evaluator will attend ExCom meetings quarterly. The ExCom will ensure science, education, and diversity objectives are met, identify and resolve conflicts, and assess resource reallocations. A full-time Institute Manager will organize activities and track success through a project Dashboard. The Institute will have a part-time

administrative assistant to the Institute Manager (provided by Woodwell; see Facilities).

A three-person **Advisory Board** comprised of experts in all constituent fields will attend the annual symposium and contribute oversight in interdisciplinary science (Wingfield; former Asst. Director, NSF Biology Directorate), diversity, and inclusion, outreach, and education (Bowser; elected 2023 AAAS Fellow), and eco-evolutionary processes (Hendry, internationally recognized expert; Tier 1 Canada Research Chair). An **Evaluator** will assess progress toward the Institute goals and will share progress with the entire team at the annual *Science Meetings* to identify pathways to improvements.

**LEADERSHIP AND MENTORING:** The EvoME leadership team has deep experience in the Arctic system, more than 200 years of Arctic research among us, the disciplines of this proposal, and leadership of large complex projects. PI Deegan has led Arctic research teams for 35 years and was co-PI of the Arctic and Plum Island LTERs. Urban has worked in the Arctic for 15 years and leads the UConn Center for Biological Risk and the Team-TERRA NRT. Boelman has worked in the Arctic for 20 years, is co-PI of the Arctic LTER, and is a leader of NASA's Arctic Boreal Vulnerability Experiment program (AboVE). Wegrzyn directs the Institute for Systems Genomics and is a leader in using genomic bioinformatics across multiple taxa to examine evolution and environmental change. Neill has worked in the Alaskan and European Arctic and brings expertise in communications through his work with journalists and his newspaper editorials. Golden has 15 years of experience at Toolik, including coordinating remote research. To provide future leadership opportunities, we plan: (1) a director transition from Deegan to Urban after Y3; (2) early career leadership mentoring of five Assistant Professors and five postdocs as WG co-leaders, with co-leaders transitioning to leaders after Y2; (3) postdocs leading the Team Science WG, with mentoring by Deegan and Weathers.



**MANAGEMENT OF EDUCATION AND OUTREACH ACTIVITIES:** Urban, Wegrzyn, and Boelman will lead development of the cross-institutional *Integrating Biology* course (UConn will provide release time for Urban and Wegrzyn) and Boelman will coordinate with Columbia's Center for Teaching and Learning to create an on-line version. Project Manager Golden will lead the REU program at Toolik. Neill and Goldstone will lead outreach activities with journalists and students. Westley will coordinate outreach communication with the U. Alaska's Intl. Arctic Research Center and Natali will coordinate communication through the Woodwell Permafrost Pathways project.

**LOGISTICS:** EvoME will leverage the unparalleled NSF-supported Arctic field logistics (See Logistics Support letter for an estimated \$4+ million in field logistics support), Toolik Field Station, Arctic (at Toolik) and Beaufort Lagoons (at Utqiagvik (Barrow) and Prudhoe Bay) LTER sites, and multiple PIs' decades of experience conducting research projects at these sites.

**FACILITATION OF INTEGRATION:** EvoME's focus on one Arctic meta-ecosystem and the concentration of interactive field work at Toolik in summer will foster strong team interactions. We include four other broad mechanisms to foster integration (Table 1, Fig. 1b). **(1) Science Meetings, Colloquia, and Team Science Retreats.** We will hold an annual all-EvoME in-person *Science Meeting* to facilitate trust, exchange information, and provide continuity in developing ideas, all of which are done most effectively

**Table 1. Integration, Education and Broadening Participation Activities.**

I=Initial, Y=Yearly, W=Winter, S=Spring, Q=Quarterly. Numbers are people in the activity.

| Activity                                          | Year | 1 | 2  | 3  | 4  | 5  | 6  |
|---------------------------------------------------|------|---|----|----|----|----|----|
| <b>Integration Mechanism</b>                      |      |   |    |    |    |    |    |
| 1a. Science Meetings                              |      | F | W  | W  | W  | W  | W  |
| 1b. Colloquia                                     |      | Q | Q  | Q  | Q  | Q  | Q  |
| 1c. Team Science Retreats                         |      | S | S  | S  | S  | S  | S  |
| 1d. National Science Symposia & Workshops         |      |   |    | Y  |    |    | Y  |
| 2a. Integration Incentive Fund                    |      |   | 1  | 2  | 3  | 3  | 2  |
| 2b. Fellowship Awards                             |      | 1 | 1  | 1  | 2  | 2  | 2  |
| 3a. Integrating Biology & Biologists Course       |      |   | 15 | 15 | 20 | 20 | 20 |
| 3b. Eyes on the Arctic REU course                 |      |   | 6  | 6  | 6  | 6  | 6  |
| 3c. <i>Behind the By Lines</i> Journalist Course  |      |   | 6  | 6  | 6  | 6  | 6  |
| 3d. Notes from the New Arctic Integrative Stories |      |   | Y  | Y  | Y  | Y  | Y  |
| 4. Working Groups & WG Meetings                   |      | Q | Q  | Q  | Q  | Q  | Q  |
| <b>Tracking Mechanisms</b>                        |      |   |    |    |    |    |    |
| 1. Dashboard Tracking of Milestones               |      | I | Q  | Q  | Q  | Q  | Q  |
| 2. Network Analysis of Integration                |      | Y | Y  | Y  | Y  | Y  | Y  |
| 3. Quantifying Team Diversity                     |      | Y | Y  | Y  | Y  | Y  | Y  |

*Science Retreat* each year. The *Retreat* will teach awareness of inclusiveness and diversity, and develop policies on ethics, data sharing, authorship, and conflict resolution (see 6. Education, Training and Diversifying).

**(2) Integration Incentive Fund and Fellowships.** We include an *Integration Incentive Fund* (IIF) for discipline-crossing research initiated by graduate students because a reward structure can facilitate team goals, and graduate students with their own funding produce more breakthrough publications<sup>63</sup>. To increase diversity among researchers, *Fellowship Awards* will provide seed funding to support scientists in underrepresented groups to develop complementary research projects.

in person<sup>63</sup>. We will also have Zoom available to ensure broad participation and inclusion. The meeting will include: keynote talks; WG reports; science talks, planning, and synthesis sessions; viewing and discussing of student- and journalist-produced communication pieces; and interactions with the Evaluator and Advisory Board. The annual meeting will rotate among institutions and be open to community audiences and journalists. At national meetings, we will develop an interdisciplinary symposia and host frequent smaller sessions and workshops annually. Annual webcast *Colloquia* will feature speakers who represent underrepresented minorities (URMs) and different scientific disciplines. Because trust, shared vision, communication, mentoring, and conflict management are necessary to build successful teams<sup>63,64</sup>, the entire team will meet in-person at a *Team*

**(3) New Integrated Courses.** We will create: (1) a new cross-institution *Integrating Biology and Biologists* graduate course; (2) a field *Eyes on the Arctic* REU program; and (3) a first-of-its-kind hands-on *Biology Behind the By-lines* science communications course with reciprocal mentoring by journalists and students that will produce *Notes from the New Arctic* integrative stories and social media posts.

**(4) Working Groups:** Research WGs and their interlocking structure with data, team science, and broader impact WGs will facilitate science integration, manuscript development and execution, communication, and inclusion. We will have a Data Manager in addition to Genomic Institute (UConn) data and pipeline support (See Data Management Plan) in the Data Integration WG. As EvoME science develops, we will hold open workshops with the broader scientific community. In recognition that everyone can contribute ideas, but everybody cannot work on everything, WG participation will have an “hourglass” shape with three stages: (1) Planning: each WG will solicit broad input to develop goals, plans, and ways to connect to other WGs; (2) Execution: smaller groups will conduct specific activities; (3) Integration: WG members will engage with the greater team to interpret and integrate results. Wide participation during the planning and integration phases will foster cross-fertilization while not hampering work execution. WGs will hold calls monthly and conduct quarterly meetings using collaborative software (e.g., Slack groups, Zoom, Google Docs, GitHub) to enhance teamwork.

**MILESTONES, AND EVALUATION:** Regular evaluation of research, education, and outreach will ensure constant learning and improvement across the Institute. We will build regular milestones into the Dashboard to evaluate research progress, integration, diversity, education, and outreach (Table 1). Evaluation will use multiple techniques (see 6. Education, Training and Diversifying) focused on the overarching question: *How effectively does EvoME promote interdisciplinary research, cooperativity, inclusion, and communication?* We will use formative and summative assessments to evaluate: (1) research productivity, and if research projects span disciplinary boundaries to create results more than the sum of their parts; (2) how well EvoME expands awareness of diversity and attracts new and diverse partners; (3) the extent to which EvoME develops scientists who increase integration in biology; and (4) how well EvoME communicates integrated research.

**Integration:** We will use systems network analysis<sup>65</sup> to assess increases in research integration and cooperativity. We aim to double cooperativity as measured by collaborative links/possible links (current network connectance=0.14), mean degree distance (current=2.8), and compartmentalization (current=0.15). We will assess interdisciplinarity of EvoME published papers with a goal of publishing three articles per project per year spanning  $\geq 3$  disciplines. We will compare this against a baseline of a random subset of pre-EvoME PI publications. We will increase integration by co-advising graduate students (two advisors from different disciplines), joint publications, and laboratory rotations, and we will evaluate temporal change in connectivity of *Integration Incentive Fund* proposals.

**Diversity and Inclusion:** Our team is diverse across gender (14 females, including lead PI, and 4 of 6 members of the ExCom), underrepresented groups (3 individuals), career stage (9 Full, 3 Associate, 5 Assistant), and university designations (3 EPSCoR, one Minority Serving Institution and one Primarily Undergraduate Institution). Our team includes three who were the first in their family to attend college, and two females and one male who obtained PhDs after children who will provide role models for alternative pathways to success. Our goal is to add two scientists from underrepresented groups by Y3 and four by Y5, to increase student diversity across all levels to 40% of our students from an average in STEM of 20% by Y3, and maintain this diversity through Y6.

**Reducing Risks:** The dashboard will capture narratives about mitigating circumstances and contingency plans to help manage risks and guide plan modifications. Risks, such as site relocation, weather, and lagging field, lab or data analysis, will be reduced by discussing challenges in open sessions at the *Science Meeting* before each year’s fieldwork. Contingencies that require resource re-allocations (e.g., relocating sites) will be openly discussed, and a consensus decision will be developed based on separating people from the problem, using objective criteria, and focusing on a shared research agenda<sup>66</sup>. The external advisory board will also provide guidance on reducing risks.



#### 4. RESEARCH ACTIVITIES

**RESPONSE TO PREVIOUS REVIEWS**—Our prior proposals received 13 excellent/very good scores and two reverse site visits. Overall, the panels were “*very excited about the project, research, management, and training and outreach plans.*” Panelists were enthusiastic that the proposed institute would perform “ambitious,” “innovative,” “truly integrative,” “exciting, important, and timely” research that “has significant potential to be transformative in “an ideal research system” and is “well-integrated with education, training, and outreach activities. Broader impacts were considered “strong,” “well-developed,” and “well-integrated.” The last panel, however, felt there were two remaining issues. First, we were too ambitious in the number of thermal regions we proposed to work in (initial = five, including one outside of the Arctic for comparison). To address this, we have reduced our sampling to three Arctic regions that still represent the range of temperature and potential connectivity (gene flow) barriers needed to test our hypotheses. These regions are all within approximately 3 hours’ drive of Toolik Field Station, which will facilitate logistics. Second, some panelists felt that by using a reduced representation of the genome (ddRADseq), we might miss important genomic regions. The cost of Whole Genome Sequencing (WGS) has declined and pipelines to process this data have been developed by PI Wegrzyn and O’Neill (a newly added molecular biologist to our team), and thus we now propose to use the full power of WGS for all genomic assessments (landscape variation, common garden and transplant experiments).

#### WHY AN INSTITUTE?

Many researchers study the role of evolution and genetics in individual species ecology and in individual ecosystems, but the Evolving Meta-Ecosystems Institute provides a unique opportunity for synthesis by integrating across different biological subdisciplines, in multiple organisms, at different trophic levels, in different kinds of ecosystems, in a region of the world that is changing rapidly. Our vision for EvoME (Fig. 1a) synthesizes understanding of the spatial variability of natural selection and the genetic basis of organismal traits, demography at the population level, and species interactions at the community level to determine their influence on ecosystem and meta-ecosystem dynamics. To accomplish this, we need researchers who specialize at each level of biological organization but who also

##### Box 1: Why the Arctic?

**Extremely fast warming.** The Arctic is warming four times faster than the Earth as a whole<sup>1-5</sup>. We can study acute and rapid evolutionary changes caused by natural selection and their ecological responses in real time.

**The system is tractable.** The low species and functional diversity of the Arctic<sup>6,7</sup> results in a few key species having disproportionately large ecosystem impacts<sup>10,11</sup> and allows us to focus the genomic and experimental work on a few species, increasing the power of detecting casual factors.

**The landscape** has a thermal gradient and potential connectivity barriers, including warm-water springs as extreme examples of potential future ecosystems, to test hypothesis about adaptation and gene flow.

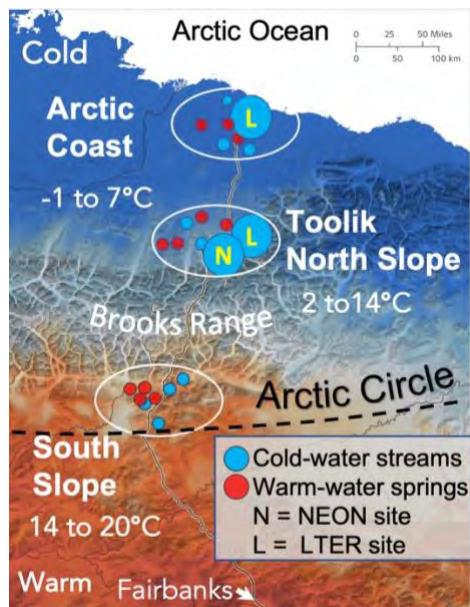
**Stream-riparian meta-ecosystems** are globally important linked meta-ecosystems. The global expansion of taller riparian willows is one of the strongest signals of Arctic warming<sup>12-14</sup> and affects reciprocal transfers of energy and resources between streams and riparian tundra ecosystems.

**The research is feasible:** Our team has *two centuries* of cumulative Arctic experience, deep collective knowledge of all proposed field sites and their species, and demonstrated success studying their genomics, traits, populations, and ecosystems.

**The work is transferable:** We will leverage simple systems under stress to understand and integrate biological responses. We will develop a theoretical and empirical template and models for studying eco-evolutionary resilience of ecosystems applicable to any meta-ecosystem.

have experience integrating across them. By concentrating on trophic subsidies, each researcher’s focal system and expertise naturally intersects with all others. By involving predictive modelers at early stages, we will build models collaboratively to develop synthetic insights as well as for feedback into designs of observations and experiments. Finally, we will synthesize research, education, and outreach to promote an environment where each informs the other and supports their success. An Institute is the appropriate mechanism to achieve this vision as it allows a high diversity of researchers to work on a common goal; it allows the flexibility to adjust work plans based on new insights and data from other projects; and it provides long-term funding to accelerate progress.

**ARCTIC OPPORTUNITY:** We take advantage of the Arctic coast and the North and South slopes of the Brooks Range (Box 1) to examine three distinct thermal and connectivity regions (Fig. 3). Between May and August (growing season in the Arctic), mean high temperatures range from -1 to 7°C near the Arctic coast, 2 to 14°C on the north slope at Toolik Field Station, and from 14 to 17°C on the south slope. The terrain is split by the Brooks Range (east-west belt of 1500-2000m mountains) which divides streams into those that flow north into the Arctic Ocean and those that flow south and west and likely acts as a high, cold connectivity barrier for most other species.



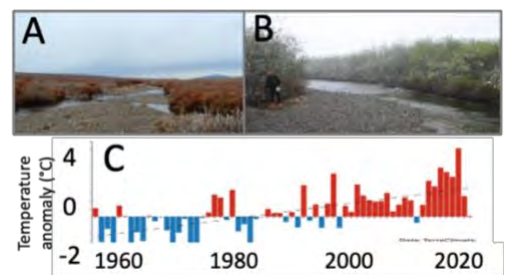
**Fig. 3. Arctic Opportunity.** Blue/red layer is annual temperature (Terraclimate) superimposed on topography. Cold-water stream and warm-water spring riparian meta-ecosystems are distributed throughout the Arctic.

research has considered how stream-riparian meta-ecosystems will be affected, nor how evolution of organisms dependent on willows will resist or facilitate whole-biome changes in the Arctic.

Stream-riparian meta-ecosystems are universally characterized by strong trophic subsidies<sup>52,72-79</sup>. Consistent with global assessments, our work in the Arctic has demonstrated terrestrial-aquatic trophic subsidies with reciprocal fluxes of energy via insects and detritus-subsidizing terrestrial birds<sup>80-82</sup> and fish<sup>11,80,83</sup>. These meta-ecosystems may be especially sensitive to climate change due to differences between aquatic and terrestrial ecosystems and how organisms in each adapt to environmental change<sup>84</sup>. To understand the resiliency of existing trophic subsidies in Arctic river-terrestrial meta-ecosystems, we will track full community changes in both aquatic and terrestrial ecosystems. Warmer climates are predicted to alter species assemblages, including new species colonizing and replacing existing species. However, the adaptive evolution of existing species has the potential to change those dynamics<sup>85</sup>. In the Arctic, the low diversity of species, extreme winter climates,

We leverage insights from unique warm-water spring systems within the frigid Arctic slope, which are part of larger river networks and important winter refuge for wildlife, as potential examples of future warm Arctic stream-riparian meta-ecosystems. Within each region, numerous warm-water springs occur where groundwater (1–8 °C) emerges aboveground to create perennially flowing streams despite winter air temperatures (< -40 °C<sup>67</sup>) that cause normal tundra streams to freeze solid<sup>68</sup>. Our team has sampled aquatic and terrestrial meta-ecosystems from Fairbanks to the Arctic Ocean, including both cold-water and remote warm-water spring meta-ecosystems. We used data from LTER and NEON sites and our prior work to target four representative cold-water streams and four representative warm-water springs in each region that will be the focus of EvoME (Fig. 3).

Globally, the clearest biological signal of Arctic warming is a conspicuous pan-arctic expansion of shrubs, including the increasing height of existing willow species along rivers (Fig. 4)<sup>12-14</sup>. This “greening of the Arctic” is among the **world’s most important large-scale ecological responses to global climate change** and is expected to cause widespread biome-level change from sedges, grass and small shrubs to extensive tall shrubs across the Arctic by 2050<sup>69,70</sup>. Yet, few researchers have considered how shrub expansion will affect associated organisms<sup>13,71</sup>, and no



**Fig. 4. Global expansion of tall riparian willows** of the same species responding to warming has been documented by Liljedahl et al. 2020. A) Typical willow stature near Toolik. B) Tall willows at a spring area. C) Temperature anomaly in Toolik region. Data from TerraClimate; Graph from Permafrost Pathways.

and the difficulty of crossing the Brooks Range will likely limit range expansions. Although we will sample carefully for evidence of range-expanding species, we will focus on the plasticity and adaptation of current species.

We focus on the five most important species involved in stream-riparian food webs and trophic subsidies: (1) Felt-leaf willow (*Salix alaxensis*), a dominant streamside plant responding to climate change by growing taller and bushier; (2) an aquatic mayfly (*Baetis bicaudatus*); and (3) a terrestrial ground-beetle (*Stereocerus haematopus*). Both insects are primary consumers and can comprise >80% of available insect biomass; (4) Arctic grayling (*Thymallus arcticus*), often the *only* fish in 1,000s of miles of Arctic streams and a secondary consumer that feeds heavily on mayflies as well as terrestrial beetles that fall into streams<sup>11,83,86</sup>. (5) White-crowned sparrows (*Zonotrichia leucophrys*) nest and forage on beetles in riparian shrubs in spring but switch to feeding on emerging stream mayflies in summer<sup>82,87</sup>. Although we will conduct field surveys to characterize spatial variation in the traits of sparrows, it is not feasible to do genomics or experimental work on them in the Arctic as their populations are both sparsely distributed and the density of individuals within populations is low relative to more southern ecosystems.

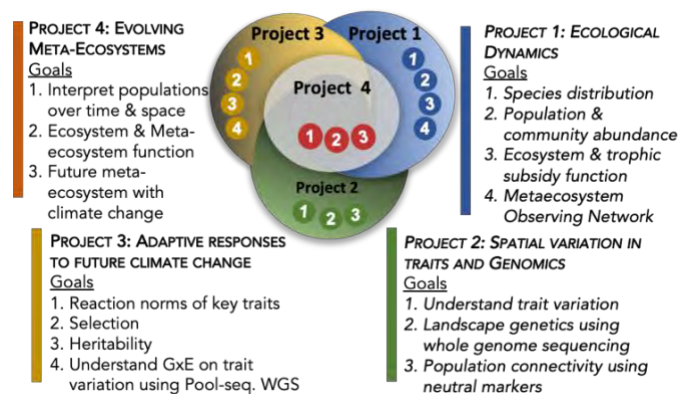
### WHICH NEW ARCTIC WILL WE SEE?

**Our overall goal is to understand how the interplay of trait plasticity and adaptive evolution by key species operating through intermediate levels of organization determine the resilience of stream-riparian meta-ecosystem ecosystems to climate warming.**

We will achieve this overall goal by integrating four projects, each with independent goals and outcomes (Fig. 5, and Project descriptions below) that are coordinated across projects and planned (Table 2) to ensure that critical data are available to inform and revise subsequent sampling activities. For example, in Y1 we will perform initial genomic and ecological surveys for the 3 regions and identify locations for transplant and ecosystem experiments, and long-term monitoring that begin in Y2. Y1 collections also will be used to assemble reference genomes for the willow, mayfly, and beetle, to assess trait variation for Project 2, and will be used to initialize models Project 3.

**PROJECT 1: ECOLOGICAL DYNAMICS:** *How do warmer conditions affect trophic subsidies to influence population, community and ecosystem processes and meta-ecosystem function?*

**Goal:** To understand how populations, communities, and ecosystem function



**Fig. 5. Project integration and research goals and outcomes.** Each project provides exchanges data and informs other projects.

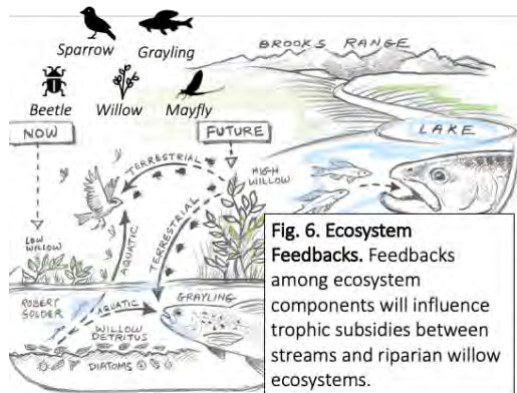
**Table 2. Timeline of Research Project Activities**

I = Initial site selection, installation, pre-manipulation measurements; C=collect individuals; E= experimental treatment and measure; B=build facility, genome or model; M=measure; P= parametrize; V= validate; T= test; A= analyze.

| Activity/Year                                                 | 1 | 2 | 3 | 4 | 5 | 6 |
|---------------------------------------------------------------|---|---|---|---|---|---|
| <b>Project 1: Ecological Dynamics</b>                         |   |   |   |   |   |   |
| Sample three thermal-connectivity regions                     | I | M | M | S | S | S |
| Execute Trophic subsidy experiments                           | I | I | E | E | E | E |
| Develop Meta-ecosystem Monitoring Network                     | B | I | P | V | V | V |
| <b>Project 2: Spatial Variation in Traits and Genomics</b>    |   |   |   |   |   |   |
| Measure traits                                                | I | M | M | M |   |   |
| Assemble Reference genome and annotate                        | C | B |   |   |   |   |
| Assess genomic variation                                      | C | T | T | T |   |   |
| Determine population connectivity                             |   |   | T | T | T | T |
| <b>Project 3: Adaptive responses to future climate change</b> |   |   |   |   |   |   |
| Conduct common garden and transplant experiments              | I | E | E | E |   |   |
| Determine reaction norms                                      |   | T | T | T | A | A |
| Measure heritability and selection                            |   | T | T | T | A | A |
| Relate extreme trait variation to genomics                    |   | M | M | M | A | A |
| <b>Project 4: Evolving Meta-Ecosystems</b>                    |   |   |   |   |   |   |
| MEME models for species to ecosystems                         | B | R | R | V | V | V |
| Future meta-ecosystem dynamics                                |   |   |   | T | T | T |

vary across thermal-connectivity regions and determine the degree to which trophic subsidies underpin meta-ecosystem function.

**Overview:** Feedbacks among different levels of biological organization are key to understanding how climate change will alter ecosystem functions. Warmer climates may increase local productivity and strengthen riparian trophic subsidies, but feedbacks or constraints on adaptation may decrease trophic subsidies (Fig. 5). We have demonstrated that taller willows support higher abundances of terrestrial insects<sup>71,87,88</sup>, suggesting that beetle subsidies to streams could increase as willows gain in stature. Sparrows will gain more foraging and nesting habitat<sup>13</sup>, potentially increasing sparrow production and reliance on emerging aquatic insects. However, current models of willow expansion and growth assume *only* that they are controlled by temperature<sup>89,90</sup>. But some willow traits (e.g., shoot numbers and growth rate) are locally adapted to other environmental factors<sup>91,92</sup> such as soil nutrient availability; thus, willow height and biomass might not change unless warming accelerates biogeochemical cycles. Further, as shrub canopies increase in size and complexity, new intra-canopy light gradients will reallocate resources (leaf N, photosynthetic proteins, pigments) and potentially lower food quality for invertebrates or decomposers. Decreases in basal food quality could lower the subsidy by decreasing insect productivity and energy density<sup>93</sup>. Additionally, warmer temperatures can shunt plant C into respiration<sup>94</sup> and increase maintenance metabolism of ectotherms, resulting in metabolic meltdown<sup>95</sup>, where energy required exceed food availability, thus lowering growth rates and production<sup>96</sup>.



**Fig. 6. Ecosystem Feedbacks.** Feedbacks among ecosystem components will influence trophic subsidies between streams and riparian willow ecosystems.

Across the three regions, we will measure ecological dynamics (Table 3, Fig. 6), including tracking population and full community assemblages, assessing productivity across trophic levels, and determining the degree of trophic subsidies to the aquatic and terrestrial riparian ecosystems. We will manipulate trophic subsidies across meta-ecosystems to test how changes in trophic subsidies alter meta-ecosystem dynamics. These dynamics will be compared to trait and genomic variation in *Project 2* to understand how this variation affects ecosystem processes.

**Roles:** Urban will lead comparisons across regions. Deegan will lead the ecosystem experiments. Boelman and

Urban will develop a Meta-ecosystem Observing Network (MEON). Experts will conduct specific measurements: Atkinson, aquatic insects; Lozier, terrestrial insects; Heskell, willow biology; Schoen, Westley, Arctic grayling; Boelman, willows, sparrows; Neill, terrestrial biogeochemistry; Deegan, food webs, trophic subsidies, aquatic biogeochemistry. Everyone will participate in data analysis and interpretation.

**H1.1: Trophic subsidies to streams will be higher on the south slope compared to the north with a distinct break at the Brooks Range associated with sharp declines in streamside willow stature (4 m in on south slope, 1 m at Toolik, <0.5 m at Arctic coast).** The most straightforward prediction is that the trophic subsidy will vary in proportion to streamside willow biovolume. To test this, we will measure population and community dynamics, assess productivity at multiple trophic levels and ecosystem functions related to productivity, decomposition, and nutrient cycling, and determine the reciprocal trophic subsidies. By comparing willow productivity to litter fall in streams, we will determine if the fraction of terrestrial primary productivity to streams varies with willow

**Table 3: Measurements of ecological dynamics.** All references are from the work of EvoME researchers.

**Population:** Abundance, individual growth, survivorship, production<sup>6,13,83,87,97-101</sup>

**Community:** Species interactions, functional communities<sup>7,13,71,88,100,102-107</sup>

**Food web:** Diets, connectance, functional, plant source, trophic level & niche space<sup>10,13,58,79,82,87,100,105,108-115</sup>

**Ecosystem:** Primary and secondary production, energy and nutrient flow, ecosystem respiration, net and gross ecosystem production, decomposition<sup>6,76,88,104,113-133</sup>

**Meta-Ecosystem:** Openness/connectedness via trophic subsidies, total meta-ecosystem (aquatic and terrestrial combined) production<sup>49,58,76,79,82,93,108,134,135</sup>



biovolume as predicted. We will compare this pattern to stable isotope niche metrics<sup>110</sup> of insects, fish, and birds to determine if food webs are more efficient under warm conditions<sup>136</sup>. We will combine this information with respiration and consumption traits (*Project 2*) to assess food-web efficiency and compare food-web niche hypervolumes<sup>110,137,138</sup> to assess if metabolic adaptation or changing diets<sup>136</sup> prevent metabolic meltdown.

*Environmental conditions and remote site observations.* We will develop a remote observing system the Meta-ecosystem Observing Network (MEON) to measure environmental conditions (i.e., weather, in-stream water level, DO, chlorophyll, temp, and pH), and some ecosystem processes (Table 4), and enable more frequent observations in remote areas. We have pioneered remote monitoring in the Arctic and will validate automated, continuously monitored data from sensors with on-the-ground data collection. MEON will make automated observations of multiple taxa (Table 4) via coupled time-lapse photography, bioacoustics, and automated tag detection to measure phenology of life history and behavior<sup>139-142</sup>.

*Boelman* has already developed state-of-the art deep learning models that determine Arctic songbird and insect phenological events from bio-acoustic recorders<sup>143,144</sup> and phenocams<sup>88</sup>.

*Methods:* Species, population, and community abundance (4 times each growing season) will be estimated using standard methods (Table 1). All species will be identified, their diets determined, and functional feeding groups assigned. Traits (Table 4 - See Project 2) will be measured on focal species. Measurements of ecosystem function including productivity, decomposition, riparian soil biogeochemistry, stream chemistry and metabolism and trophic subsidies (Table 3).

**H1.2: The decrease of trophic subsidies will disproportionately affect secondary production in rivers because fish depend more on trophic subsidies than do birds.** The power of large-scale experiments lies in their ability to capture complex ecosystem responses and, when combined with process-level studies and hypothesis testing, to test for interacting effects that occur only at the ecosystem-scale<sup>145-147</sup> and generate insights not obtained any other way<sup>7,116,148,149</sup>. We will conduct three whole ecosystem experiments to obtain fundamental understanding of the importance of the subsidy to meta-ecosystem function: 1) *Decrease* the two-way *trophic subsidy* on whole meta-ecosystem reaches (200 m reach; n=4 treatments and 4 reference sites; block leaf fall and insect emergence using mesh hoop covers<sup>48,150</sup>); 2) *Increase willow litter* to mimic expansion (200 m reach; n=4 treatments and 4 reference sites). Based on results from *Projects 2 & 3*), 3) we will conduct 3) a meta-ecosystem manipulation by transplanting south slope warm-adapted willows to cold-water north slope streams to test the impacts of the migration of new genotypes with different phenotypic expression into the Arctic on fish, birds, and insects<sup>151</sup>.

We predict that reduced trophic subsidies will alter stream food webs more than terrestrial food webs because willow leaves provide nutrients to oligotrophic streams. We predict that increased litter will increase stream metabolism and nutrient cycling, and thus increase aquatic production and the aquatic-to-terrestrial subsidy. We have shown that grayling exhibit strong site fidelity to feeding locations, and food declines result in lower growth rates and survival<sup>152,153</sup>. Sparrows can forage in upland areas to replace lost stream subsidies<sup>87</sup>, suggesting that behavioral responses can buffer energy acquisition and fledgling growth from trophic subsidy declines. This work provides knowledge connecting short-term behavioral responses (adult foraging) to population dynamics (juvenile fish or bird growth) across generations<sup>154,155</sup>.

*Methods:* We will measure multiple species and ecosystems responses (Table 3, 4) and foraging behavior of grayling (*Deegan*) and sparrows (*Boelman*) using Lotek Nanotags and antenna arrays<sup>156,157</sup>.

**PROJECT 2: LANDSCAPE VARIATION IN TRAITS AND GENOMICS:** *How well-connected are populations and how do energy-related traits vary across spatial thermal gradients and gene flow barriers?*

**Goal:** To determine population connectivity and how traits associated with acquiring, allocating and spending energy and nutrients vary across the thermal-connectivity landscape and are related to generation times and dispersal capacity for key species.

**Overview:** Recent work suggests that adaptations of key traits can be as important as changes in species composition in influencing ecosystem rates of nutrient cycling, production and decomposition<sup>158</sup>. When organisms *are* the cross-ecosystem fluxes, these phenotypic changes can substantially alter meta-



ecosystem function. For example, if warming decreases body size because of increased metabolism but abundance stays the same, the trophic subsidy will decrease.

We will combine both neutral and adaptive landscape genomics to characterize the processes influencing different components of genetic trait variation. The landscape genomics approach uses high-quality genome-wide markers, putative selection pressures for georeferenced individuals, and deep sampling across the landscape that reflects representative demographic and evolutionary histories<sup>9</sup>. We will examine if selection acts primarily on standing genetic variation or on new variants and if similar genes/regions are evolving in parallel across populations and estimate the effect sizes (and types) of putative adaptive loci. This landscape-wide approach will be combined with common gardens (*Project 3*) to associate genomic variation with phenotypic variation. Sequencing pools of 20 individuals from trait distribution tails from the common gardens will enable more robust and cost-effective assessment. The common garden/transplant component is time-consuming but remains the best method to separate out genotype by phenotype by environment interactions.

We will determine how traits associated with acquiring, allocating and spending energy and nutrients vary across the thermal-connectivity gradients (Table 4). We will estimate landscape genetics and gene flow from neutral genomic markers using Whole Genome Sequencing (WGS - Box 2). We will determine if trophic subsidies and traits change together or in opposition by linking results to measured abundances and trophic subsidies from *Project 1*. To determine relatedness and population connectivity (via gene flow), we will relate traits to landscape genomics<sup>9,159,160</sup>.

**Roles:** O'Neill and Wegrzn will lead genomics analysis of all species and work with experts on taxa who will measure the traits: Atkinson, aquatic insects; Lozier, terrestrial insects; Heskell, willow; Schoen, Arctic grayling; Boelman and Krause, sparrows; Neill, terrestrial nutrient cycling in association with willows. Everyone will participate in data analysis and interpretation.

**H2.1: Populations will vary in their phenology, growth, metabolic rates, and survivorship across the spatial-thermal gradient in ways that match local conditions.** Across the gradient, we will measure

“functional traits”, which affect performance, (Table 4) for all five focal species and “effect traits”, which affect ecological properties beyond the organism<sup>23,183</sup>, such as productivity, decomposition and nutrient cycling<sup>140,184,185</sup> (Table 4). Stoichiometric principles suggest that traits affecting allocation, production, respiration, and excretion can influence ecosystem nutrient processing<sup>186,187</sup>. The capacity of ectotherms (fish, insects) to increase food intake faster than respiration will determine if a warming world enhances growth and productivity or induces metabolic meltdown<sup>95,188</sup>. We will contribute new insights into theories of stoichiometry and bioenergetics related to intraspecific trait variation that may reveal trade-offs between energetic performance and active metabolism<sup>186,187,189,190</sup>.

**Methods:** Traits (Table 4) will be measured on all five focal species. For willow transplant experiments, we will assess the effect of genotype<sup>191</sup> on soil nutrient cycling (N mineralization, and decomposition; see H1.2) as potential feedback on willow growth and meta-ecosystem function.

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**Table 4. Life-history, phenological, morphological, and eco-physiological traits** related to demography, energy allocation, reproductive efficiency, and species interactions. Traits will be measured in surveys under natural conditions and in common garden and transplant experiments.

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**Life history:** *Willow:* Survival (germination, seedling, adult), age of maturity, fecundity; *Mayfly, Beetle, Grayling, Sparrow:* Survival (larvae, adults), age of maturity, fecundity, voltinism<sup>87,109,152,161,162</sup>

**Phenological:** *Willow:* Bud burst, flowering, leaf out, and leaf senescence; *Mayfly, Beetle:* Date of emergence from soil or stream, metamorphosis, aestivation; *Grayling, Sparrow:* Migration arrival and departure, breeding, days to hatch and emergence or fledge<sup>71,102,103,163,164</sup>

**Morphological:** *Willow:* Shrub biovolume, height, Specific leaf area; *Mayfly, Beetle, Grayling, Sparrow:* Body-mass index, size at metamorphosis<sup>20,46,97,105,165-168</sup>

**Eco-physiological:** *Willow:* Thermal tolerance, photosynthesis, APAR, respiration, water and nutrient use efficiency, growth rate, stoichiometry (C, N, P); *Mayfly, Beetle, Grayling, Sparrow:* Thermal tolerance, respiration, growth rate, excretion rate, energy density (kcal/g), stoichiometry (C, N, P), habitat choice<sup>20,58,98,110,166,169-180</sup>

**Species interactions:** *Willow:* Pollination, herbivory; *Mayfly, Beetle, Grayling, Sparrow:* Trophic level, Diet plasticity<sup>13,71,80,88,97,100,101,104,105,143,153,181,182</sup>

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**H2.2: We predict stronger spatial genetic differentiation and a stronger genetic discontinuity across the Brooks Range in species with limited dispersal, decreasing the potential for regional evolutionary rescue from warm-adapted southern populations.** Regional gene flow can promote evolutionary rescue by supplementing local populations with genotypes pre-adapted to local changes or by creating novel genotypes by mixing genetic backgrounds<sup>192,193</sup>. We will use the power of the whole genome sequencing (WGS) approach (Box 2) to estimate population genetic measures of variation and gene flow<sup>9,194</sup>. The landscape genomics implemented at whole-genome resolution using genotype-environment association approaches, will inform landscape variability and gene flow barriers<sup>195-198</sup>. Common gardens and transplant experiments for the same species will be used to refine estimates of heritability through comprehensive trait evaluation and Pool-seq WGS<sup>15,199</sup> (Project 3).

We predict a genomic break between the north and south slopes, with further differentiation by watersheds for all species. Grayling<sup>200</sup>, mayfly<sup>201</sup> and beetles<sup>202</sup> disperse via river networks, and as no watersheds flow north over the Brooks Range, they have limited potential for gene flow from southern populations. Warm spring sites are connected to other cold-water systems; thus, we predict some genetic mixing between warm-springs and cold-water streams. Our pilot research<sup>203</sup> using ddRADseq suggests genomic divergence in grayling within and across watersheds, indicating the proposed 40 individuals per site, together with the power of WGS, will provide robust gene flow estimates across a larger area.

**Methods:** We will conduct WGS on willow, mayfly, beetle, and grayling across the thermal-connectivity landscape with 40 individuals from 8 populations (4 warm-springs, 4 cold-stream systems, 3 locations within each system) in 3 regions (3,840 libraries). To obtain the most accurate population-level assessments for these four non-model organisms, we will generate 3 (mayfly, ground-beetle, and willow) high-quality reference genomes to complement the one available for grayling. The 3,840 libraries will be short-read sequenced at 20X based on current genome-size estimates. For genome assemblies, one individual will be sequenced to 60X long-read coverage (Oxford Nanopore or PacBio) and 100X short-read coverage (Illumina), *de novo* assembled and structurally annotated to define protein-coding gene space<sup>204-209</sup>. We will include neutral genetic structure directly as a covariate in redundancy analysis (RDA) which considers polygenic responses to a multitude of environmental metrics as well as high resolution environmental data<sup>210</sup>.

**PROJECT 3: ADAPTIVE RESPONSES TO FUTURE CLIMATE CHANGE: Can existing plasticity or local adaptation of key traits maintain ecosystem function during climate change?**

**Goal:** To understand the plasticity and potential for adaptive evolution of traits across current and future climates via common garden and transplant experiments.

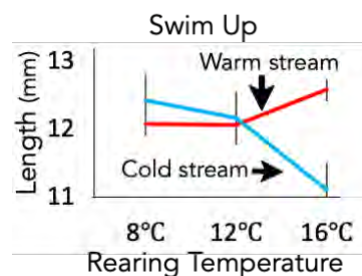
**Overview:** We examine the underlying mechanisms of functional trait variation, which ultimately shapes the dynamics of populations, trophic subsidies, and meta-ecosystem functions (*Themes 1, 4*). We deploy experiments and genomics, capitalizing on the strengths of each approach and synthesizing results to build a foundational understanding of how key Arctic species will respond to climate change. Existing

**Box 2: Leveraging whole genome sequencing for non-model species.**

- Advances in methods and decreased costs now put the most reliable high-throughput genotyping method - whole-genome sequencing (WGS) - within reach for non-model organisms. By sequencing all bases of a genome many-fold, WGS effectively uncovers all of the genetic information in a genome, including alleles that might be of high importance under future conditions yet are currently rare in a population<sup>8,9</sup>.
- Compared to reduced representation techniques like ddRADseq WGS enhances the power to detect genotype-trait associations, especially in populations where low levels of linkage-disequilibrium exists.
- WGS yields the most extensive set of markers and densest genotyping, thereby improving estimates of relatedness, gene flow, and the genetic differentiation of complex traits. It is also possible to obtain estimates of heritability under natural conditions without the need for pedigrees, or complex mating experiments.
- Using WGS in combination with efficient Pool-seq methods enables in depth understanding of potential loci underlying extreme phenotypes from common garden and transplant experiments<sup>9,15</sup>.

phenotypic plasticity (e.g., thermal performance curves) might allow populations to persist during climate change, but not always. When climate change exceeds plasticity, additive genetic variation (e.g., heritability) might fuel rapid adaptations and evolutionary rescue. Moreover, gene flow from nearby populations can enhance genetic variation, especially when arriving from warmer habitats<sup>211</sup>. This standing genetic variation, along with generation length and population size, will determine if adaptive evolution can keep pace with the rapid climate change in the Arctic<sup>212</sup>. Common garden and reciprocal transplant experiments between contrasting environments will assess local adaptation and phenotypic plasticity<sup>213,214</sup>. When combined with whole genome sequencing, they can decipher complex relationships between phenotype, genotype, and the environment and the genetic basis of key traits.

**Roles:** Urban will lead GXE experiments and work with taxon experts who will conduct common garden and transplant experiments: Atkinson, aquatic insects; Lozier, terrestrial insects; Wegrzn, Heskell, Neill, willow; Westley, Schoen, Deegan, Arctic grayling. O'Neill and Wegrzn will lead genomics. Bolnick will provide expertise and data analysis programs; Bret-Harte will help design the willow experiments and coordinate placement at Toolik. Everyone will participate in data analysis and interpretation.



**Fig. 7. Reaction norm for a life history trait (swim up) for Arctic grayling from cold and warm streams measured in our common garden experiment.**

**H3.1: Plasticity will enable rapid shifts in phenotypes that maintain fitness under future climate change and thereby maintain ecosystem function.** We predict that adaptive plasticity will match current climate regimes but will be insufficient under future climate conditions<sup>212</sup>. We will measure trait-environment relationships (= reaction norms; Fig. 7) across current and future climates in controlled common garden experiments and across the natural climate gradient via transplant experiments. We focus on traits (growth, survival, metabolism) that parameterize the MEME models (*Project 4*). We will develop trait-performance curves from transplant experiments to assess the fitness consequences of measured plasticity<sup>215</sup>.

**Methods:** Common garden experiments for willow, mayfly, beetle, and grayling will be located at Toolik in temperature-controlled Aquatic Common Garden and Terrestrial Greenhouse facilities purpose-built for EvoME, where we will raise individuals from different families in different thermal environments; cool (8°C); typical Arctic summer at Toolik (12°C); and future climate (16°C = +4°C predicted climate change). Transplant experiments occur at one warm/cold site at each of the 3 thermal-connectivity regions. We will measure traits and performance on all experimental populations.

**H3.2: Evolution via natural selection will enable shifts in phenotypes that maintain fitness under future warm climates and thereby maintain ecosystem function.** We predict that standing genetic variation will not be sufficient to facilitate adaptive evolution that matches the pace of climate change in species like grayling with long generation times and small population sizes, but could be sufficient in species like mayfly and beetle with short generation lengths and large population sizes<sup>212</sup>. We will estimate natural selection and additive genetic variation to estimate adaptive responses of traits (Table 4) in the common garden and transplant experiments described above.

**Methods:** We will measure *selection* on a subset (n=20) of phenotypically divergent individuals from the performance trait distribution tails (e.g., body size) from common garden experiments, then challenge them with hot future climate conditions using performance traits (growth and survival) to assess selection. We expect selection to be multidimensional and therefore we will employ methods that estimate partial and correlated selection<sup>216,217</sup>. From these “hot challenge” experiments, we will select the most phenotypically divergent individuals in key performance traits (e.g., survival, growth) under future climate treatment and use powerful and cost-effective Pool-Seq WGS to evaluate unique genomic variation associated with climate performance traits. Each pool of 20 individuals will be collected from the extreme tails of trait distributions and sequenced at 20X coverage for each pool. Variant detection will be performed with MAPGD<sup>15</sup>. Local adaptation will be quantified by analyzing phenotype-environment associations to determine the degree to which environmental measures are reflected in

both phenotype-environment and genotype-environment analyses. These data will also allow us to test for correspondence between traits and genomic variation observed across the landscape (*Project 2*). We are not looking for *every* adaptive allele, but rather to identify markers of potentially adaptive evolutionary units of large effect that could be refined through future genetic manipulations. If we find corresponding genomic regions involved in adaptive traits and those traits and alleles also occur in wild populations in warmer regions, but not in colder regions, then we will further define genomic regions linked to trait variation and selection. We predict that populations from warm-spring systems will have the most potential to supply adaptive alleles to moderate dispersers such as willows and grayling, but that the potential for rescue of more restricted dispersers (mayfly and ground-beetle) will be limited.

For common garden experiments, we will raise individuals from full- and half-sib families in the different thermal environments described above to estimate heritability for each population and thermal environment. Reciprocal transplant experiments between regions and spring sites within a region provide estimates of genetic variation and performance under realistic conditions. In common-gardens, we will estimate genotype-by-environment interactions by family to understand if plasticity has the potential to evolve. We will employ parallel, but variable designs, to estimate heritability. For grayling, we will employ nested full-/half-sib analysis by stripping eggs from females and fertilizing subsets with different males as done in prior work (Fig. 7). For willows, we will estimate narrow-sense heritability on clonal cuttings from different parents (20 populations of genotyped individuals, 1m x 5m plots, in greenhouses at Toolik). For beetles and mayflies, we will perform full-sib analyses by raising separate families from eggs (5-10 replicates). For full-sib analyses, we assume a broad-sense heritability ( $h^2$ ) of 0.25<sup>218</sup> and standard approximations for optimal design<sup>219</sup>, to set the number of individuals to  $\sim 2/h^2 = 8$  and  $N = 25$  families for each population for a total ( $T=nN$ ) of 200 individuals. The sampling variance for this design is estimated at 0.02 with 90% power to detect a non-zero heritability. We will use mixed random forest models to provide robust estimates even of low heritabilities for polygenic traits<sup>220</sup>.

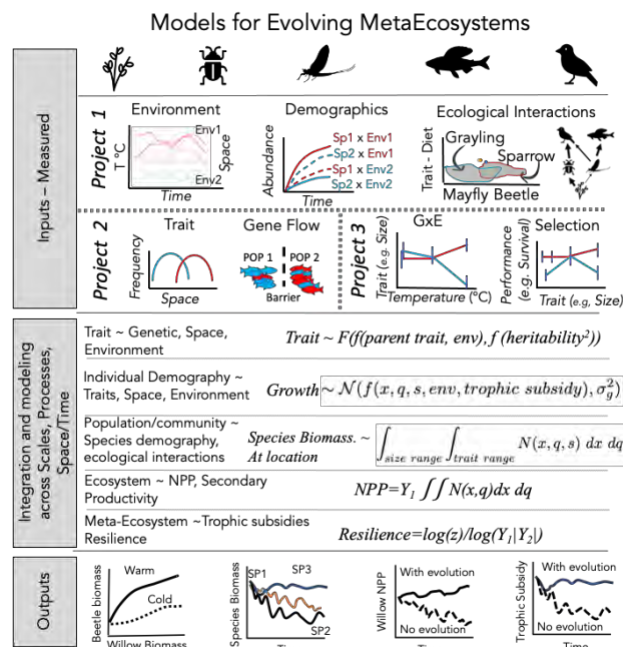
**PROJECT 4: EVOLVING META-ECOSYSTEMS:** *How will plasticity and evolutionary adaptation interact to rescue and maintain terrestrial-aquatic ecosystem coupling and meta-ecosystem function across landscape scales? How well can we project future changes in the Arctic?*

**Goal:** To synthesize and validate meta-ecosystem dynamics based on organismal traits and their relationship to ecosystem and meta-ecosystem function, and forecast future function based on the relative plasticity and adaptive potential of populations along the thermal gradient.

**Overview:** We have developed a modular modeling approach called Models of Evolving Meta-Ecosystems (MEMEs) that can accommodate multiple species, mechanistic sub-models, and climate data streams to identify future scenarios of how evolution affects meta-ecosystems. By synthesizing observations, experiments, and models, we aim to reveal not just direct connections between ecology and evolution, but also any complex feedback loops or dead ends that we can then design future studies to test. To ensure our predictions and forecasts are robust, we will validate models built using EvoME and MEON data with independent and extensive datasets collected by Arctic LTER and NEON sites.

**Roles:** Merow and Urban will lead the modeling and work with taxon experts (Atkinson, aquatic insects; Lozier, terrestrial insects; Heskell and Boelman, willow; Schoen, Westley, Deegan, Arctic grayling; Boelman and Krause, sparrows; Neill, nutrient cycling) who will provide the data needed to parameterize, calibrate and validate models. Everyone will participate in data analysis and interpretation.

**MEMEs:** MEMEs are based on the trait-centric approach of Trait Driver Theory (TDT)<sup>59-61</sup>, which provides an efficient and tractable way to link individual traits to population, community, and ecosystem properties (Fig. 7). TDT usually describes community dynamics, but we have pioneered ways in which its trait-based principles can also include evolution. Models for all taxa (each described by trait distributions) are linked in MEMEs through their common currencies of traits and biomass. Traits are then linked to performance via resource allocation tradeoffs. MEMEs connect ecosystems and trophic interactions through Integral Projection Models (IPMs) which describe how individual growth, survival, and fecundity (*Project 1*) depend on traits, genetics, and environments (*Projects 2, 3*). We have developed IPMs extensively<sup>221-223</sup> and will extend them<sup>224</sup> to include environmental and genomic variability. We will use



**Fig. 8. Models of Evolving Meta-Ecosystems uses as inputs measured organismal traits, genomic variation from Project 2, performance, heritability and selection from Project 3, and demographics and ecological interactions across trophic levels from Project 1 to understand the future Arctic with and without evolution. Equations are examples for different levels. Graphs are examples of EvoME data that will be used in models.**

parameters<sup>227</sup> and apply climate scenarios to forecast short- (10Y) and long-term (80Y) changes in meta-ecosystem function. By linking species, trophic levels, and ecosystems, we will transcend current eco-evolutionary work to understand how evolution affects entire meta-ecosystems.

## THE FUTURE OF EVOME

EvoME will integrate biological scales and processes from the fundamental building blocks of life (genes) to Earth's life-sustaining meta-ecosystems, thus contributing to a broader and more predictive understanding of a Grand Challenge of Biology: how biological systems interact over space and time to respond to rapid environmental change. We will do this in relatively simple Arctic ecosystems to ensure rapid progress in understanding the structure and dynamics of the most rapidly warming biome on Earth.

After 6 years, we will have created a framework for integrative research that unites research and researchers across disciplines, techniques, and scales to build knowledge within a tractable system. Just as importantly, we will have created a community of biology integrators that have learned to work together across disciplines and scales to arrive at new knowledge and share that knowledge with students, broader audiences, and local communities. We will expand our network of monitoring stations across the Arctic to improve models and integrate them with real-time data to inform future research opportunities and hypotheses. We will also be prepared to test hypotheses and contribute to better conservation biology efforts<sup>228</sup>. For instance, if we transplant willows from warmer locations, will we observe discernible effects on stream subsidies? Do fish from warm-adapted populations do better than remnant populations when introduced into streams warmed by climate and what are the ecosystem impacts? We will also anticipate and prepare for new species in the Arctic, including salmon and beaver, which are expanding their ranges. Our trait-based model should predict ecosystem impacts of colonizing species given what we learned about the current species. Finally, by creating an institute in which we interact with the wider scientific community we will extend our framework to trophic subsidies in other systems to learn which parts are generalizable and which are specific to our system.

individual-based simulations to verify results, but by applying IPMs, we have the potential to speed up analyses and derive more general principles. For example, we developed an initial model of willow adaptation and its effect on trophic subsidies to streams. Without evolution, a warming climate produced smaller willows, which decreased net primary productivity and stream subsidies (Merow, in prep.). When willows could adapt respiration, they became larger and stabilized subsidies.

**Methods:** We will parameterize MEMEs with trait and fitness variation measured within and among populations and regions (*Project 2*). Trait variation is a function of genetics and plasticity and G x E, as estimated by experiments and genomic assays (*Project 3*). Heritability, G×E interactions, selection, and gene frequency estimates will contribute to rate calculations for adaptive evolution. Additional species and their functional traits will be determined by ecological surveys. We will then link trait variation to trophic subsidies and ecosystem function (*Project 1*). We will use Approximate Bayesian Computation<sup>225,226</sup> to estimate individual-level demographic rates inversely from population or community



## 5. RESEARCH RESOURCES

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### LEVERAGED RESOURCES

**Arctic Data Center:** NSF- center designed to preserve and discover NSF-funded science in the Arctic, including permanent online data storage, metadata, software, and documents. We will create a Data Portal and Project landing page that will organize, curate, visualize and make our data discoverable.

**NSF Polar Programs Logistics Support.** The Arctic logistics support (Support Letter; \$4M Rough order of Magnitude estimate provided) will provide safety training, vehicles, snow machines, helicopters, user-days at Toolik, remote camps, boardwalks, and build the Common Garden and Greenhouse facilities at Toolik.

**Toolik Arctic Field Station:** Over 100 scientists from around the world and many disciplines work at Toolik, the only NSF Arctic field station, providing a rich intellectual environment. Toolik provides housing, meals, laboratories, GIS and mapping, technical and IT assistance, and shared equipment.

**LTER/NEON Network:** We will add new insect, bird, fish and genomics to the Arctic and Beaufort Lagoons LTERs and NSF NEON Network to track change in aquatic and terrestrial ecosystems.

**Permafrost Pathways** (Woodwell): Sue Natali's TED Audacious Project (~\$40M, six-years) will expand measurement and process modeling of pan-Arctic permafrost thaw. EvoME will benefit by joint discussions, co-location of sites, strengthened Alaska Native recruiting, parallel development of dashboards to track progress across complex projects, and enhanced Arctic focused public facing communications.

**Polaris Project** (Woodwell): Natali (NSF IUSE) will facilitate diversity recruitment and retention of undergraduates and provide a path from the month-long Polaris experience to longer term REU to graduate school experiences for underrepresented groups.

**Oasis or tomb?** (Wildlife Conservation Society, Alaska). Deegan and Heidi Golden (Woodwell) are collaborators on this US Fish and Wildlife project to understand winter habitat dynamics and ecology of fishes and scavengers at perennial springs on Alaska's North Slope. We will share sites and data.

**Unstableground.org:** This Woodwell/ESRI partnership is an interactive data visualization hub that explores how Arctic landscapes are changing and will benefit EvoME students and outreach by providing visualization support and an outlet for their work.

**Permafrost Discovery Gateway:** (Woodwell) Liljedahl will facilitate interactions with her "Navigating the new Arctic tundra through Big Data, artificial intelligence, and cyberinfrastructure Gateway". Data and AI approaches to analysis will be shared.

**Team-TERRA NRT** (UConn): Urban leads a transdisciplinary NSF NRT in which EvoME students can participate in understanding landscape risk analysis.

**Tamamta - All of Us NRT** (U. Alaska Fairbanks): Westley elevates the role of Indigenous knowledge in graduate training in natural resources and will support at least one EvoME Indigenous graduate student.

**National Climate Adaptation Science Center** (Woodwell). Deegan will facilitate participation in the national USGS CASC network's Climate Adaptation Scientists of Tomorrow Program, a new training initiative that will help prepare undergraduate students from historically underrepresented backgrounds for leadership positions in climate adaptation science.

**AK DaTUM RCN-UBE** (NSF, UAK). We will contribute data and opportunities to improve Alaska undergraduate education for Indigenous, rural, and non-traditional students.

**URoFL:EN** (UConn): Does re-wilding lead to re-wiring of gene expression and species interaction networks? Bolnick's project examines the evolution of a fish and ecological networks by introducing a fish into fishless lakes in Alaska and will share new tools in computer science and statistics designed to test for plastic and evolutionary changes in genetic, transcriptomic, and ecological networks.

**URoL: Epigenetics 2** (UAlabama): Bumble bee cold tolerance across elevations - From epigenotype to phenotype across space, time, and levels of biological organization. Lozier's project will share genomic

and epigenetic perspectives and computational techniques to determine thermal tolerance of invertebrates along environmental gradients.

**Alaska Native Science & Engineering Program:** Westley will coordinate student recruitment with ANSEP, which since 1995 has facilitated Alaska Natives in 6th grade to the PhD from over 100 communities by placing students with mentors and providing funding for opportunities.

**Summer internship for Indigenous peoples in Genomics Consortium (SING):** Bolnick will facilitate Indigenous student participation in SING, whose goal is to include as many Indigenous communities, tribal students, and leaders as possible in genomics.

**CartograPlant:** Wegryzn's (PI, USDA) CartograPlant web application (integration of genotype, phenotype, and environment) will be used for landscape genomics/association mapping of georeferenced, phenotyped, and sequenced plants.

**ABoVE:** Boelman and Griffin (PIs NASA Arctic Boreal Vulnerability Experiment Program) participate in projects that will provide ABoVE-produced open-source data to look for areas of rapid shrub expansion to sample for genomics and traits.

**Arctic Today:** Harvard University/Woodwell program provides opportunity to expand outreach through Arctic Today—a widely distributed source of online news and analysis about the Arctic's changing economy and environment across the circumpolar North.

**Botanical Information and Ecology Network (BIEN):** Merow's Advances in Biological Informatics grant creates a generic workflow for scaling up species ranges and will benefit our trait-based modeling to test theories about range expansion in the Arctic.

**Institute for Systems Genomics: Computational Biology Core (UCONN):** Wegrzyn's (Director) ISG will provide infrastructure support for research and training in genetics, genomics and bioinformatics, and data management and storage of the whole genome sequencing.

**Data Science Institute (Columbia University):** Boelman and Urban will continue to collaborate with DSI on AI training sets and data analysis for the Meta-Ecosystems Observing Network (MEON).

**Center for Biological Risk:** Urban is the Director of The Center of Biological Risk, which seeks to improve the capacity to assess, manage, and communicate biological risks of global change. The Center will assist in training graduate students in prediction, management, and stakeholder communication.

#### **NOVEL RESEARCH RESOURCES MADE AVAILABLE TO THE COMMUNITY**

**Aquatic Common Garden Facility:** This facility (ACGF), designed and built by Battelle Polar Services engineers (cost is included in the logistics support request), will be a state change in the aquatic experimental capacity at Toolik.

**Plant and Consumer Trait Databases:** We will contribute our plant and animal trait data to free and open trait databases available (TRY for plants; FishBase for fish; Movebank for migration and foraging traits; Freshwater Biological Traits Database for macroinvertebrate taxa).

**Genome Assembly and Annotation:** Wegrzyn is a member of the annotation standards committee for Earth BioGenome Project which provides training in assembly/annotation. Annotated Genomes will be shared with Earth BioGenome Project and the Whole Genome Shotgun collection of GenBank.

**Phenological data from cameras:** We will upload our data to the PHENOCAM Network data portal, which is an NSF-funded open network for tracking phenological change using cameras and will share our pipelines for processing the data on GitHub.

**Ecological data at LTER/NEON sites:** We will contribute all ecological data collected at three LTER sites to site databases following LTER protocols and metadata standards.

## BROADER IMPACTS

### 6. EDUCATION, TRAINING, AND DIVERSIFYING

Our goal is to develop a research team that will be diverse, and that will take EvoME educational principles back to their universities and forward into their careers to integrate biological research in a diverse and inclusive manner. Key elements of successful research in interdisciplinary science<sup>63</sup>, include: (1) purposefully *expanding the diversity and retention in the research community* by recruiting and retaining team members at all levels with broad racial, gender, economic, and experiential diversity across career stages; (2) a *commitment to a shared research theme*, including deep understanding in specialties and broad understanding of integrated biology; (3) deliberate *training in Team Science* that builds interaction skills, modes of communication for a climate of inclusivity and equity; and (4) *communication among disciplines and to broad audiences*. Our education and diversification plans are designed to overcome barriers to communication among people and disciplines in team research. We use known strategies (see below) for increasing recruitment, retention, and success of diverse groups, including societally relevant problem solving, paid research internships, and culturally competent mentoring. We anticipate more than 180 students and postdoctoral fellows will be involved over 6 years (Table 5).

**Table 5. Educational Trainees.** Number of unique individuals over 6 years.

|                                                                   |     |
|-------------------------------------------------------------------|-----|
| Post-doctoral Fellows                                             | 6   |
| Research Graduate Students                                        | 12  |
| Students - Integrated Course (includes non-EvoME funded students) | 90  |
| REU Students @ Toolik Field Station                               | 30  |
| Undergraduates working in labs during the academic year           | 50  |
| Total                                                             | 188 |

Beyond the EvoME biologists, the Education and Outreach team includes: **Goldstone**, Woodwell Director of Communications, who has a science PhD and 10 years' experience with National Public Radio; **Weathers**, Past-President of the Ecological Society of America, who pioneered application of Science of Team Science to empower early-career scientists; **Olex**, who has 20 years' experience as a team-building trainer and facilitator; **Natali**, Director of Woodwell Arctic program and 2021 American Geophysical Union

Sulzman Award for Excellence in Education and Mentoring; **N. Golden**, a Black early-career Arctic scientist who is our first EvoME Fellow; **H. Golden**, who will lead the REU program, and **Liljedahl**, an expert in data visualization with 20 years of experience in Arctic hydrology.

#### SPECIFIC ACTIVITIES

##### 1. Expand Diversity and Retention in the Research Community.

**Goals:** Increasing and retaining diversity will be a marker of success for EvoME. The Dashboard will track student gender, race, ethnicity, first generation college and income. Minoritized students currently comprise 25-33% of students across our institutions. Our goal is to add two scientists from underrepresented groups by Y3 and four by Y5. Our goal is 40% students from URMs, which would be more than 50% higher than the 24% of STEM degrees currently awarded to minorities in the US<sup>238-240</sup> and maintain this diversity through Y6.

**Expanding:** We will use multiple approaches to expand faculty and student diversity. We will expand faculty diversity by inviting to our *Science Symposium* each year two speakers who are underrepresented minorities (URMs). We will provide *Fellowship Awards* to one URM per year in Ys 1-5 to participate in research. **N. Golden**, a Black early-career Arctic scientist will be our first EvoME Fellow. N. Golden is a graduate of Polaris and an example of the retention we aim to promote<sup>229</sup>. We will use connections of participants at 14 institutions to recruit URM students. These connections include a new Woodwell partnership with Howard University, contacts provided by evaluator Garritt, contacts with URM faculty who teach in Polaris and the URM-focused Woods Hole Partnership in Education Program (PEP). Polaris (undergraduate Arctic experiences, 56% URM) and PEP (100% URM) have strong URM recruiting and retention track records. Natali will coordinate with Polaris and PEP. Project PIs or N. Golden will travel to MSIs, and meetings of the Society for Advancement of Chicanos/Hispanics and Native Americans in Science, the Alaska Forum of the Environment, and Alaska Native Science and Engineering Program to recruit students. We will advertise at minority-serving institutions and in programs for minorities (e.g., SING or BLaST at U. of Alaska, Fairbanks).

All PIs will actively recruit diverse students through their home institutions. Urban will coordinate overall recruiting efforts and recruiting through UConn's memberships in the Louis Stokes Alliance for Minority Participation Network, McNair Scholars Program, and National Graduate Engineering Degrees for Minorities Consortium. Urban leads an NSF NRT and has pioneered methods to decrease implicit biases against women and minoritized students during application review<sup>230</sup>. We will implement a blind review process (in which applicant names and affiliations are hidden) for all opportunities, which reduces biases<sup>231</sup> and increases diversity in recruiting<sup>232</sup>. Urban and Westley will leverage new diversity recruitment programs being implemented through their respective graduate NRTs, and Westley and Schoen will coordinate recruitment with Alaska Forum of the Environment, and Alaska Native Science and Engineering Program. Columbia has committed to supporting full tuition and stipend for one year for two graduate students (one URM) and two undergraduate students (one URM) to participate in summer research. UConn has committed to three months of summer support for two graduate students (one URM) and an undergraduate researcher.

**Retention:** We will increase retention by creating ongoing opportunities for problem-solving, "next steps" and on-going mentoring. We focus on this approach because activities that involve real-world problem-solving, collaborative learning, and peer-to-peer mentoring improve retention of underrepresented groups<sup>233-237</sup>. We created an intentional sequence among connected early undergraduate opportunities with options that build from shorter (3-5 week) Polaris and PEP programs to a longer (9 week) *Eyes on the Arctic* program and then potentially to recruitment as EvoME graduate students.

**2. Shared Research Theme: New Courses and Funding for Graduate Research.** We plan three primary activities to create a community of integrated researchers around a shared research theme.

**First,** we will develop a graduate course, *Integrating Biology and Biologists*, led by Urban and co-taught by all co-PIs. The *Integrating* curriculum will provide content-based foundations across the disciplines of genomics, traits, ecology, and ecosystems. The course will cover cross-cutting questions, research methods, data stewardship and analysis, and navigating integrated careers. UConn will support course release for three semesters for Urban and Wegrzyn to facilitate the development of the new course. This year-long, in-classroom, and online multi-institutional course will build understanding of the shared goals of integrated biology and provide integration skills for the next generation of biologists. Class size will be kept small to facilitate the personal interactions that build trust among individuals with different backgrounds. Every year, 15-20 students, including non-EvoME funded students, will meet weekly for two hours (in-person at UConn with online participants from other institutions) followed by post-class online breakout group discussions based on "blended learning" that suggests that learning during in-class and students' own time increases comprehension<sup>241,242</sup>. We will share the course online by producing video "modules" with Columbia's Center for Teaching and Learning that offers hands-on guidance on inclusive teaching<sup>243</sup>.

**Second,** we will have a 9-week research-intensive REU experience (*Eyes on the Arctic*) that will take place at Toolik Field Station each summer at the time of maximum field research activity. H. Golden will lead the REU program of six undergraduates each year who will conduct team centered, inquiry-based research. REUs will receive a stipend. All travel, per diem, lodging, and field station charges will be paid by the grant. Undergraduates will partner with senior EvoME participants to develop scientific questions, design experiments, learn data analysis, how to write papers, and present talks. Students will present their work at a summer symposium at Toolik and we will support them to present at scientific meetings.

**Third,** we will create an *Integration Incentive Fund (IIF)* that will provide competitive grants to teams of two to three graduate students whose research fuses three biological disciplines to address EvoME questions. Team Science research has shown that including a grant reward structure can facilitate team goals and that graduate students or postdocs with their own funding are associated with higher levels of breakthrough publications<sup>63</sup>. These teams can include outside graduate students to expand EvoME's reach. The IIF adopts the best features of the NSF Doctoral Dissertation Improvement Grant Program in which modest funding enables student-initiated research. All student teams will submit proposals, and each proposal will include budget justifications and a two-minute pitch video produced in the *Biology*

*Behind the By-Lines* Course (see Outreach) We will convene a review committee of faculty, postdocs and (after year one) former IIF recipients.

**3. Training in Team Science.** We will hold an annual three-day *Team Science Retreat* of team members at all levels (students, postdocs, and faculty) that will focus on methods to create a highly interactive, safe, and inclusive work environment in the lab and the field<sup>244-246</sup>. This *Retreat* will be co-led by Weathers and Olex, both of whom are pioneers in the Science of Team Science<sup>64,66</sup>. Weathers will lead about data sharing, authorship, ethics, plagiarism, peer review, and authorship. We will discuss aspects of team science including legacy structures of academia, sources of support, rewards and incentives, success metrics, motivations for collaboration, and differences in credit practices among disciplines<sup>63</sup>. Olex will lead discussions and interactive role playing on intangibles like communication<sup>247</sup>, difficult conversations, giving feedback, power and personal relationships (including harassment), accountability, emotional intelligence and trust<sup>66</sup>. The *Retreat* will provide formal training in the Responsible Conduct of Research that identifies the challenges of working at remote field sites, establishes roles and responsibilities, creates regular mechanisms for communication and check-ins, and defines organizational mechanisms for reporting and responding to issues of harassment. Each participant will commit to an EvoME Code of Conduct (see Section 8). Participants will also receive additional harassment training from Toolik via online tutorials that are required before working at the field station. The *Retreat* will conclude with lab and field safety training conducted by NSF Polar Logistics support (see letter).

**4. Communication.** In the first of its kind, we will create a hands-on experience — *Biology Behind the By-lines* — in which students and journalists will be paired for co-mentoring. Journalists will mentor students in communicating concepts to people not in their field and students will mentor journalists in conducting science (See Outreach for more details). This will break down the longstanding cultural barriers between the press and scientists and enhance communication across boundaries. We will link education to outreach by requiring student teams to develop two-minute video pitches co-produced with journalists to apply for IIF grants. Teams will create content for *Notes from the New Biology*, a part of the Outreach Plan. Participants will submit articles to *Arctic Today* online news (see Leveraged Resources).

## ASSESSMENT

To assess and improve Education, Training, and Diversification outcomes, evaluator Garrett will annually conduct formative (pre-activity) and summative (post-activity) interviews and surveys<sup>248</sup> with trainees (students, postdocs) and mentors in the REU program, Team Science Retreat, Biology Behind the By-lines and the Science Symposium. Garrett will meet twice each year with the ExCom and the whole team to discuss findings. This information will be used to inform decisions about how to improve. These assessments will be based on a logic model of self-efficacy, which determines how individuals think, motivate, and perform, which is linked to success and persistence<sup>249</sup>. Garrett will conduct interviews and surveys based on her prior work and metrics and instruments (Table 6) developed with the ExCom. This will assess participants' understanding of integrated biology and best practices of team science (cognitive gains) and will ask participants to reflect on how their participation has changed their perceptions and whether we have achieved a climate of inclusion and equity (affective gains, mindfulness and intent). Mentors will be asked how their participation has impacted their own actions or beliefs. Fellows who receive grant funding will be interviewed to understand if the grant funding achieves our goal, and how the outcomes of their projects align with our mission. Garrett will do longitudinal interviews to identify factors that enhance interdisciplinarity and retention.

**Table 6. Education, training and diversifying evaluation metrics and instruments.**

### Metrics-Interdisciplinarity

Productivity and papers

Discipline-bridging projects

Integrative papers

Integrative student grant proposals

Project cooperativity

### Metrics-Team Science and Diversity

Self-efficacy gains

Team diversity

Personnel awareness of Institute goals

Sense of community and belonging

Expectations for contributions

### Instruments

Documentation of papers, presentations

Pre and post activity evaluative surveys

Pre and post activity interviews

Network analysis

Assessment of social media posts



## 7. OUTREACH ACTIVITIES

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### OVERVIEW

Our outreach activities will engage the scientific community in integrated research around the issue of rapid climate change and increase public science literacy through activities that have multiple points of intersection with education activities (Fig. 1b).

**1. Scientific Community Engagement:** Our EvoME website will provide in-depth information on science and provide new opportunities for new faculty and students. To encourage interactions among a broad range of scientists, we will host four webcast *Colloquia* each year that feature invited speakers. We will prioritize speakers from diverse backgrounds (within biology and URM) who will be selected and hosted by students and postdocs. Speakers will give presentations and lead discussions on challenges that require integrating disciplines in biology. The lectures will be webcast and students will participate in a one-hour webcast discussion moderated by the student host. *Colloquia* will be archived online for asynchronous viewing. We have dedicated funding for *Colloquia* speakers to spend time at Toolik or a participating institution, and to interact with and then potentially join EvoME as *Fellows*. We will also hold an annual *EvoME Science Meeting*. The meeting will rotate among institutions and be open to other scientists, the public and journalists to facilitate participation from beyond EvoME. Faculty and students will participate broadly in traditional scientific meetings including organizing special meeting sessions and larger *Symposia*.

**2) Biology Behind the By-lines.** To improve communication about the multiple levels of biological organization that influence meta-ecosystems, we will create a first of its kind program in which professional journalists, students, and mentors work together to enhance each other's communication skills. Dissemination of findings and interpretation of the implications of biology has traditionally fallen to journalists or artists and it is critical that they understand the origins and implications of new insights from integrated biology<sup>250</sup>. In addition, today's new media creates unprecedented opportunities for scientists to communicate directly with wide audiences<sup>251,252</sup>, but few scientists receive specific education in how to explain science to today's internet- and social media-focused public. Our two-week, hands-on intensive science immersion course for six Science Journalism Fellows each year at Toolik led by Co-I's Neill and Goldstone will be integrated with a communications immersion experience for graduate students and postdocs that will train them to interact with journalists and directly communicate their science to audiences through print, radio, and video. Trainees will be mentored by Anna Liljedahl on data visualization of complex GIS data sets.

This activity is modeled after a course Neill taught to journalists at multiple LTER sites for 14 years and that Neill and Deegan taught at Toolik in 2008–2010. Our experience is that hands-on science broadens journalists' perspectives. For example, Jane Qiu, who covered Asia for *Nature*, told us that she reported on methane releases from Chinese dams and authored an award-winning series on the effects of climate change on the Tibetan Plateau based on what she learned in our Toolik course. A committee of scientists and journalists will select journalist participants from diverse backgrounds and across print, radio and visual media, and student and postdoc participants across disciplines and institutions.

A new dimension to the program is that Journalism Fellows and students will engage in co-mentoring—journalists mentoring students in their communication specialty, students mentoring journalists in their scientific specialty. Journalists, students, and postdocs will travel, go in the field, and work in the lab together. The journalists will analyze, interpret, and present data that they themselves collect in four “modules” drawn from the core questions and experiments, crossing themes from genomics, evolution, and ecosystems. Journalists will have one full day of sample collection for each module, they will perform laboratory analyses, analyze and interpret data, and present to the Toolik community. From Toolik, all trainees and journalists will travel to UConn where they will continue the hands-on curriculum and perform data analyses in biology and genomics that integrate across EvoME projects. We will emphasize how molecular biology and data science integrate the genetic, evolutionary,

and ecological responses to rapid climate change. Journalists will work hands-on to interpret genomic datasets and present their findings in a final open workshop.

Time will be dedicated for student-journalist pairs to create a student-produced print, radio or video feature, or op-ed stories designed to communicate their new integrative biological science findings to the public. Graduate students and postdocs will be required to produce pieces for the *Notes from the New Biology* blog (see below). Graduate students will work with journalists and mentors to produce the two-minute video pitches to apply to the *Integration Incentive Fund*. *Eyes on the Arctic* REU students will be engaged in structured discussions with journalists, graduate students and postdoc about communicating science, and are required to produce regular posts to social media.

**3. Notes from the New Biology.** To reach the broad public, we will create a curated Facebook page, blog, Twitter, and Instagram feeds (managed by H. Golden) with posts by students and faculty and stories facilitated by Goldstone. These will report on key activities, new experiments, and new findings and serve as an outlet for the stories students produce from *Integrated Science Communication* and *Eyes on the Arctic*. Early-career students will be mentored by postdocs and graduate students.

**4. Rural Community Outreach.** Goldstone, Schoen, Westley and Natalie will expand existing efforts by EVoME scientists to communicate with rural Alaska communities through radio in Bethel (KYUK) and North Slope (KBRW). We focus on radio because, in addition to Facebook and other social media, it is a critical mode of communication for remote communities where the internet is not available. The International Arctic Research Center and College of Fisheries and Ocean Sciences have existing relationships with reporters versed in radio and print media that are always keen to cover climate and fisheries related issues affecting Alaskans. Additionally, EVoME team members will also conduct listening sessions in the Arctic community of Utqiaġvik (coordinated by Westley who has existing contacts) and other Native Alaskan communities (coordinated through Natalie's Permafrost Pathways Project) and attend the *Alaska Forum of the Environment* to gain local and Indigenous perspectives on Arctic environmental change and to generate future science-themed radio stories.

## ASSESSMENT

EVOME evaluator Garret will conduct pre- and post-activity surveys and interviews of journalists and students using the same formative and summative assessments that we will use for educational activities. We will evaluate both the extent of biological integration in outreach activities and the success and impact of outreach elements (Table 7). To evaluate integration across biology, we will develop metrics that quantify how many levels of biology are integrated in the outreach pieces and in the research projects on which they are based. We will quantify both journalist- and student-written, spoken, and posted pieces and use metrics of circulation and web hits to estimate impact. We will also track the number of blogs, Twitter, and Instagram posts each year using our dashboard. Garret will perform interviews each year with EVoME team members and follow-up interviews with students who participate in *Biology Behind the By-Lines* and *Notes from the New Biology*. The data generated from the assessments and interviews will inform decisions about how to improve our outreach.

**Table 7. Outreach activities evaluation metrics and instruments.**

|                                                                                                                            |
|----------------------------------------------------------------------------------------------------------------------------|
| <b>Metrics-Interdisciplinarity</b>                                                                                         |
| Interdisciplinarity of written, radio and blog pieces                                                                      |
| <b>Metrics-Success of elements</b>                                                                                         |
| Number of written stories and web hits                                                                                     |
| Number of radio stories and web hits                                                                                       |
| Number of Twitter and Instagram posts and hits                                                                             |
| Extent to which production of communication pieces for non-scientists by students and faculty continues after the programs |
| Extent to which EVoME faculty incorporate communication for non-scientists into teaching and mentoring                     |

## 8. INTELLECTUAL CONTRIBUTION AND CREDIT

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EvoME's community is large, interdisciplinary and includes scientists at all career stages. We therefore developed the following draft guidelines that will help avoid misunderstandings that can hinder scientific discovery and training and that will promote diversity, inclusion and interdisciplinarity. These guidelines will be refined and confirmed by EvoME members at our *Science Meeting* and *Team Science Retreats*. In addition, we will: (1) address differences in practices among disciplines related to credit in our annual *Team Science Retreat* and (2) use existing resources for practical guidance, including CRediT (Contributor roles Taxonomy) used by many journals to establish individual author contributions, reduce disputes and facilitate collaboration<sup>64,66,253</sup>

**Management of Rights and Credits.** EvoME members at all levels will develop a Scope of Work (SOW) at the start of the Institute that outlines their responsibilities and anticipated products. This will be updated annually as EvoME research advances. SOWs will be discussed at Annual meetings and in Working Groups. The 'hour-glass' method (See Project Management) of sharing data across the Institute provides opportunities for integrating projects and publications. If a team member wishes to use EvoME data, models, or other tools, at the exploratory stage a working title, abstract and description of data to be included will be submitted to the ExCom and shared with the PIs for discussion. The Scope of Work serves as a guide for which PI (including their postdocs and students) is responsible for a given publishable topic. Scientists can be authors when they (1) achieve intellectual and active participation in manuscript preparation and any one or more of the following: (2a) Substantial contribution to study conception (proposal and experimental design); (2b) Project execution; or (2c) Data analysis and interpretation. Principal Investigator (PI or co-I) status alone does not grant authorship. Individuals will automatically be asked to confirm authorship if they contribute data, models, or other tools. All authors have a responsibility to keep the manuscript moving forward and must approve the final draft of the manuscript before submission. Working Group meetings in which manuscripts are discussed and the interlocking structure with data management best practices will facilitate timely manuscript development.

All trainees (undergrads, grads, postdocs) who contributed substantially to the work should be included as authors. Authorship order will be decided by discussion among the authors as the first part of paper development. The Institute does not espouse any particular philosophy of author order, although it is typical that the first author will be the researcher who has done the most to advance the work. Where people have equal claim, the order may be determined by a fair procedure (e.g., alphabetically or randomization) agreed upon in advance. Conflicts can be discussed in Working Groups or in smaller groups with a group of non-involved PIs or the Executive Committee.

**Sharing of Information, Data, and Resources.** All research products will be collected, shared, and fully released so that collaborative work can move forward in a timely manner. We require the publication in open databases and sharing of data as soon as practical; however, students may choose to keep their thesis data out of the public domain until they have either published or have graduated. Data, field, and lab protocols, and analytical and modeling tools, will be made available broadly once they are uploaded to the archive (see Data Management Plan). Any participant can use the Institute's field and lab protocols, analytical and modeling tools developed, for publications, courses, presentations, etc. by following the guidelines described above.

We are committed to engaging with Alaska Native Communities by: (1) working with the NSF Navigating the New Arctic Community office; (2) abiding by the Woodwell Center's "Guiding Principles for Working in Northern Communities" and the IARP guidelines<sup>254</sup>, (3) exchanging knowledge by attending the Alaska Forum of the Environment and developing stories for Alaska Native Corporation community newsletters.

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