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Not for distribution

COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

PROGRAM ANNOUNCEMENT/SOLICITATION NO./DUE DATE	☐ Special Exception to Deadline Date Policy	FOR NSF USE ONLY
NSF 15-609 — 08/02/16		NSF PROPOSAL NUMBER 1655560

FOR CONSIDERATION BY NSF ORGANIZATION UNIT(S) (Indicate the most specific unit known, i.e. program, division, etc.)

DEB - Population and Community Ecology, (continued)

DATE RECEIVED	NUMBER OF COPIES	DIVISION ASSIGNED	FUND CODE	DUNS# (Data Universal Numbering System)	FILE LOCATION
08/02/2016	1	08010000 DEB	1182	073133571	09/30/2016 4:07pm S

EMPLOYER IDENTIFICATION NUMBER (EIN) OR TAXPAYER IDENTIFICATION NUMBER (TIN)	SHOW PREVIOUS AWARD NO. IF THIS IS ☐ A RENEWAL ☐ AN ACCOMPLISHMENT-BASED RENEWAL	IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? YES ☐ NO ☒ IF YES, LIST ACRONYM(S)
386006309		

NAME OF ORGANIZATION TO WHICH AWARD SHOULD BE MADE: University of Michigan Ann Arbor

ADDRESS OF AWARDEE ORGANIZATION, INCLUDING 9 DIGIT ZIP CODE: Ann Arbor, MI 481091274
US

AWARDEE ORGANIZATION CODE (IF KNOWN): 0023259000

NAME OF PRIMARY PLACE OF PERF: University of Michigan

ADDRESS OF PRIMARY PLACE OF PERF, INCLUDING 9 DIGIT ZIP CODE:
University of Michigan
440 Church Street
Ann Arbor ,MI ,481091041 ,US.

IS AWARDEE ORGANIZATION (Check All That Apply) (See GPG II.C For Definitions) ☐ SMALL BUSINESS ☐ MINORITY BUSINESS ☐ FOR-PROFIT ORGANIZATION ☐ WOMAN-OWNED BUSINESS

☐ IF THIS IS A PRELIMINARY PROPOSAL THEN CHECK HERE

TITLE OF PROPOSED PROJECT: Linking species coexistence to the functioning of communities

REQUESTED AMOUNT	PROPOSED DURATION (1-60 MONTHS)	REQUESTED STARTING DATE	SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
$ 603,617	36 months	04/01/17	1631301

THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW
- ☐ BEGINNING INVESTIGATOR (GPG I.G.2)
- ☐ DISCLOSURE OF LOBBYING ACTIVITIES (GPG II.C.1.e)
- ☐ PROPRIETARY & PRIVILEGED INFORMATION (GPG I.D, II.C.1.d)
- ☐ HISTORIC PLACES (GPG II.C.2.j)
- ☐ VERTEBRATE ANIMALS (GPG II.D.6) IACUC App. Date ______ PHS Animal Welfare Assurance Number ______
- ☒ FUNDING MECHANISM Research - other than RAPID or EAGER
- ☐ HUMAN SUBJECTS (GPG II.D.7) Human Subjects Assurance Number ______ Exemption Subsection ______ or IRB App. Date ______
- ☐ INTERNATIONAL ACTIVITIES: COUNTRY/COUNTRIES INVOLVED (GPG II.C.2.j) ______
- ☒ COLLABORATIVE STATUS Not a collaborative proposal

PI/PD DEPARTMENT: Natural Resources and Environment

PI/PD FAX NUMBER:

PI/PD POSTAL ADDRESS:
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Ann Arbor, MI 48109
United States

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CO-PI/PD				
CO-PI/PD				
CO-PI/PD				

CERTIFICATION PAGE

Certification for Authorized Organizational Representative (or Equivalent) or Individual Applicant

By electronically signing and submitting this proposal, the Authorized Organizational Representative (AOR) or Individual Applicant is: (1) certifying that statements made herein are true and complete to the best of his/her knowledge; and (2) agreeing to accept the obligation to comply with NSF award terms and conditions if an award is made as a result of this application. Further, the applicant is hereby providing certifications regarding conflict of interest (when applicable), drug-free workplace, debarment and suspension, lobbying activities (see below), nondiscrimination, flood hazard insurance (when applicable), responsible conduct of research, organizational support, Federal tax obligations, unpaid Federal tax liability, and criminal convictions as set forth in the NSF Proposal & Award Policies & Procedures Guide,Part I: the Grant Proposal Guide (GPG). Willful provision of false information in this application and its supporting documents or in reports required under an ensuing award is a criminal offense (U.S. Code, Title 18, Section 1001).

Certification Regarding Conflict of Interest

The AOR is required to complete certifications stating that the organization has implemented and is enforcing a written policy on conflicts of interest (COI), consistent with the provisions of AAG Chapter IV.A.; that, to the best of his/her knowledge, all financial disclosures required by the conflict of interest policy were made; and that conflicts of interest, if any, were, or prior to the organization's expenditure of any funds under the award, will be, satisfactorily managed, reduced or eliminated in accordance with the organization's conflict of interest policy. Conflicts that cannot be satisfactorily managed, reduced or eliminated and research that proceeds without the imposition of conditions or restrictions when a conflict of interest exists, must be disclosed to NSF via use of the Notifications and Requests Module in FastLane.

Drug Free Work Place Certification

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent), is providing the Drug Free Work Place Certification contained in Exhibit II-3 of the Grant Proposal Guide.

Debarment and Suspension Certification

(If answer "yes", please provide explanation.)

Is the organization or its principals presently debarred, suspended, proposed for debarment, declared ineligible, or voluntarily excluded from covered transactions by any Federal department or agency? Yes ☐ No ☒

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent) or Individual Applicant is providing the Debarment and Suspension Certification contained in Exhibit II-4 of the Grant Proposal Guide.

Certification Regarding Lobbying

This certification is required for an award of a Federal contract, grant, or cooperative agreement exceeding $100,000 and for an award of a Federal loan or a commitment providing for the United States to insure or guarantee a loan exceeding $150,000.

Certification for Contracts, Grants, Loans and Cooperative Agreements

The undersigned certifies, to the best of his or her knowledge and belief, that:
(1) No Federal appropriated funds have been paid or will be paid, by or on behalf of the undersigned, to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with the awarding of any Federal contract, the making of any Federal grant, the making of any Federal loan, the entering into of any cooperative agreement, and the extension, continuation, renewal, amendment, or modification of any Federal contract, grant, loan, or cooperative agreement.
(2) If any funds other than Federal appropriated funds have been paid or will be paid to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with this Federal contract, grant, loan, or cooperative agreement, the undersigned shall complete and submit Standard Form-LLL, ''Disclosure of Lobbying Activities,'' in accordance with its instructions.
(3) The undersigned shall require that the language of this certification be included in the award documents for all subawards at all tiers including subcontracts, subgrants, and contracts under grants, loans, and cooperative agreements and that all subrecipients shall certify and disclose accordingly.

This certification is a material representation of fact upon which reliance was placed when this transaction was made or entered into. Submission of this certification is a prerequisite for making or entering into this transaction imposed by section 1352, Title 31, U.S. Code. Any person who fails to file the required certification shall be subject to a civil penalty of not less than $10,000 and not more than $100,000 for each such failure.

Certification Regarding Nondiscrimination

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent) is providing the Certification Regarding Nondiscrimination contained in Exhibit II-6 of the Grant Proposal Guide.

Certification Regarding Flood Hazard Insurance

Two sections of the National Flood Insurance Act of 1968 (42 USC §4012a and §4106) bar Federal agencies from giving financial assistance for acquisition or construction purposes in any area identified by the Federal Emergency Management Agency (FEMA) as having special flood hazards unless the:
(1) community in which that area is located participates in the national flood insurance program; and
(2) building (and any related equipment) is covered by adequate flood insurance.

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent) or Individual Applicant located in FEMA-designated special flood hazard areas is certifying that adequate flood insurance has been or will be obtained in the following situations:
(1) for NSF grants for the construction of a building or facility, regardless of the dollar amount of the grant; and
(2) for other NSF grants when more than $25,000 has been budgeted in the proposal for repair, alteration or improvement (construction) of a building or facility.

Certification Regarding Responsible Conduct of Research (RCR)
(This certification is not applicable to proposals for conferences, symposia, and workshops.)

By electronically signing the Certification Pages, the Authorized Organizational Representative is certifying that, in accordance with the NSF Proposal & Award Policies & Procedures Guide, Part II, Award & Administration Guide (AAG) Chapter IV.B., the institution has a plan in place to provide appropriate training and oversight in the responsible and ethical conduct of research to undergraduates, graduate students and postdoctoral researchers who will be supported by NSF to conduct research.
The AOR shall require that the language of this certification be included in any award documents for all subawards at all tiers.

CERTIFICATION PAGE - CONTINUED

Certification Regarding Organizational Support

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent) is certifying that there is organizational support for the proposal as required by Section 526 of the America COMPETES Reauthorization Act of 2010. This support extends to the portion of the proposal developed to satisfy the Broader Impacts Review Criterion as well as the Intellectual Merit Review Criterion, and any additional review criteria specified in the solicitation. Organizational support will be made available, as described in the proposal, in order to address the broader impacts and intellectual merit activities to be undertaken.

Certification Regarding Federal Tax Obligations

When the proposal exceeds $5,000,000, the Authorized Organizational Representative (or equivalent) is required to complete the following certification regarding Federal tax obligations. By electronically signing the Certification pages, the Authorized Organizational Representative is certifying that, to the best of their knowledge and belief, the proposing organization:
(1) has filed all Federal tax returns required during the three years preceding this certification;
(2) has not been convicted of a criminal offense under the Internal Revenue Code of 1986; and
(3) has not, more than 90 days prior to this certification, been notified of any unpaid Federal tax assessment for which the liability remains unsatisfied, unless the assessment is the subject of an installment agreement or offer in compromise that has been approved by the Internal Revenue Service and is not in default, or the assessment is the subject of a non-frivolous administrative or judicial proceeding.

Certification Regarding Unpaid Federal Tax Liability

When the proposing organization is a corporation, the Authorized Organizational Representative (or equivalent) is required to complete the following certification regarding Federal Tax Liability:

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent) is certifying that the corporation has no unpaid Federal tax liability that has been assessed, for which all judicial and administrative remedies have been exhausted or lapsed, and that is not being paid in a timely manner pursuant to an agreement with the authority responsible for collecting the tax liability.

Certification Regarding Criminal Convictions

When the proposing organization is a corporation, the Authorized Organizational Representative (or equivalent) is required to complete the following certification regarding Criminal Convictions:

By electronically signing the Certification Pages, the Authorized Organizational Representative (or equivalent) is certifying that the corporation has not been convicted of a felony criminal violation under any Federal law within the 24 months preceding the date on which the certification is signed.

Certification Dual Use Research of Concern

By electronically signing the certification pages, the Authorized Organizational Representative is certifying that the organization will be or is in compliance with all aspects of the United States Government Policy for Institutional Oversight of Life Sciences Dual Use Research of Concern.

AUTHORIZED ORGANIZATIONAL REPRESENTATIVE	SIGNATURE	DATE
NAME Amy Holihan	Electronic Signature	Aug 2 2016 9:05AM

TELEPHONE NUMBER	EMAIL ADDRESS	FAX NUMBER
734-763-2171	aholihan@umich.edu	734-763-2171

COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

FOR CONSIDERATION BY NSF ORGANIZATION UNIT(S) - continued from page 1
(Indicate the most specific unit known, i.e. program, division, etc.)

DEB - Ecosystem Studies

Direct for Biological Sciences
Division of Environmental Biology
Population and Community Ecology

Proposal Classification Form
PI: Cardinale, Bradley / Proposal Number: 1655560

CATEGORY I: INVESTIGATOR STATUS (Select ONE)

- ☐ Beginning Investigator - No previous Federal support as PI or Co-PI, excluding fellowships, dissertations, planning grants, etc.
- ☐ Prior Federal support only
- ☐ Current Federal support only
- ☑ Current & prior Federal support

CATEGORY II: FIELDS OF SCIENCE OTHER THAN BIOLOGY INVOLVED IN THIS RESEARCH (Select 1 to 3)

☐ Astronomy	☐ Engineering	☐ Psychology
☐ Chemistry	☐ Mathematics	☐ Social Sciences
☐ Computer Science	☐ Physics	☑ None of the Above
☐ Geosciences		

CATEGORY III: SUBSTANTIVE AREA (Select 1 to 4)

☐ BIOGEOGRAPHY	☐ Decomposition	☐ Molecular Evolution
☐ Island Biogeography	☐ Biogeochemistry	☐ Methodology/Theory
☐ Historical/ Evolutionary Biogeography	☐ Limnology/Hydrology	☐ Isozymes/ Electrophoresis
☐ Phylogeography	☐ Climate/Microclimate	☐ Nucleic Acid Analysis (general)
☐ Methods/Theory	☐ Whole-System Analysis	☐ Restriction Enzymes
☐ CHROMOSOME STUDIES	☑ Productivity/Biomass	☐ Nucleotide Sequencing
☐ Chromosome Evolution	☐ System Energetics	☐ Nuclear DNA
☐ Chromosome Number	☐ Landscape Dynamics	☐ Mitochondrial DNA
☐ Mutation	☐ Chemical & Biochemical Control	☐ Chloroplast DNA
☐ Mitosis and Meiosis	☐ Global Change	☐ RNA Analysis
☑ COMMUNITY ECOLOGY	☐ Climate Change	☐ DNA Hybridization
☐ Community Analysis	☐ Regional Studies	☐ Recombinant DNA
☐ Community Structure	☐ Global Studies	☐ Amino Acid Sequencing
☐ Community Stability	☐ Forestry	☐ Gene/Genome Mapping
☐ Succession	☐ Resource Management (Wildlife, Fisheries, Range, Other)	☐ Natural Products
☐ Experimental Microcosms/ Mesocosms	☐ Agricultural Ecology	☐ Serology/Immunology
☐ Disturbance	☐ EXTREMOPHILES	☐ PALEONTOLOGY
☐ Patch Dynamics	☐ GENOMICS (Genome sequence, organization, function)	☐ Floristic
☐ Food Webs/ Trophic Structure	☐ Viral	☐ Faunistic
☐ Keystone Species	☐ Microbial	☐ Paleoecology
☐ COMPUTATIONAL BIOLOGY	☐ Fungal	☐ Biostratigraphy
☐ CONSERVATION & RESTORATION BIOLOGY	☐ Plant	☐ Palynology
☐ DATABASES	☐ Animal	☐ Micropaleontology
☐ ECOSYSTEMS LEVEL	☐ MARINE MAMMALS	☐ Paleoclimatology
☐ Physical Structure	☐ MOLECULAR APPROACHES	☐ Archeozoic
		☐ Paleozoic
		☐ Mesozoic

- [ ] Cenozoic
- [ ] POPULATION DYNAMICS & LIFE HISTORY
- [ ] Demography/ Life History
- [ ] Population Cycles
- [ ] Distribution/Patchiness/ Marginal Populations
- [ ] Population Regulation
- [ ] Intraspecific Competition
- [ ] Reproductive Strategies
- [ ] Gender Allocation
- [ ] Metapopulations
- [ ] Extinction
- [ ] POPULATION GENETICS & BREEDING SYSTEMS
- [ ] Variation
- [ ] Microevolution
- [ ] Speciation
- [ ] Hybridization
- [ ] Inbreeding/Outbreeding
- [ ] Gene Flow Measurement
- [ ] Inheritance/Heritability
- [ ] Quantitative Genetics/ QTL Analysis
- [ ] Ecological Genetics
- [ ] Gender Ratios
- [ ] Apomixis/ Parthenogenesis
- [ ] Vegetative Reproduction
- [ ] SPECIES INTERACTIONS
- [ ] Predation
- [ ] Herbivory
- [ ] Omnivory
- [ ] Interspecific Competition
- [x] Niche Relationships/ Resource Partititioning
- [ ] Pollination/ Seed Dispersal
- [ ] Parasitism
- [ ] Mutualism/ Commensalism
- [ ] Plant/Fungal/ Microbial Interactions
- [ ] Mimicry
- [ ] Animal Pathology
- [ ] Plant Pathology
- [ ] Coevolution
- [ ] Biological Control
- [ ] STATISTICS & MODELING
- [ ] Methods/ Instrumentation/ Software
- [ ] Modeling (general)
- [ ] Statistics (general)
    - [ ] Multivariate Methods
    - [ ] Spatial Statistics & Spatial Modeling
    - [ ] Sampling Design & Analysis
    - [ ] Experimental Design & Analysis
- [ ] SYSTEMATICS
- [ ] Taxonomy/Classification
- [ ] Nomenclature
- [ ] Monograph/Revision
- [ ] Phylogenetics
- [ ] Phenetics/Cladistics/ Numerical Taxonomy
- [ ] Macroevolution
- [ ] NONE OF THE ABOVE

CATEGORY IV: INFRASTRUCTURE (Select 1 to 3)

- [x] COLLECTIONS/STOCK CULTURES
- [ ] Natural History Collections
- [ ] DATABASES
- [ ] FACILITIES
- [x] Controlled Environment Facilities
- [x] Field Stations
    - [ ] Field Facility Structure
    - [ ] Field Facility Equipment
- [ ] LTER Site
- [ ] INDUSTRY PARTICIPATION
- [ ] Technique Development
- [ ] TRACKING SYSTEMS
- [ ] Geographic Information Systems
- [ ] Remote Sensing
- [ ] NONE OF THE ABOVE

CATEGORY V: HABITAT (Select 1 to 2)

TERRESTRIAL HABITATS

- [ ] GENERAL TERRESTRIAL
- [ ] TUNDRA
- [ ] BOREAL FOREST
- [ ] TEMPERATE
    - [ ] Deciduous Forest
    - [ ] Coniferous Forest
    - [ ] Rain Forest
    - [ ] Mixed Forest
    - [ ] Prairie/Grasslands
    - [ ] Desert
- [ ] SUBTROPICAL
    - [ ] Rain Forest
    - [ ] Seasonal Forest
    - [ ] Savanna
    - [ ] Thornwoods
    - [ ] Deciduous Forest
    - [ ] Coniferous Forest
    - [ ] Desert
- [ ] TROPICAL
    - [ ] Rain Forest
    - [ ] Seasonal Forest
    - [ ] Savanna
    - [ ] Thornwoods
    - [ ] Deciduous Forest
    - [ ] Coniferous Forest
    - [ ] Desert
- [ ] CHAPPARAL/ SCLEROPHYLL/ SHRUBLANDS
- [ ] ALPINE
- [ ] MONTANE
- [ ] CLOUD FOREST
- [ ] RIPARIAN ZONES
- [ ] ISLANDS (except Barrier Islands)
- [ ] BEACHES/ DUNES/ SHORES/ BARRIER ISLANDS
- [ ] CAVES/ ROCK OUTCROPS/ CLIFFS
- [ ] CROPLANDS/ FALLOW FIELDS/ PASTURES
- [ ] URBAN/SUBURBAN
- [ ] SUBTERRANEAN/ SOIL/ SEDIMENTS
- [ ] EXTREME TERRESTRIAL ENVIRONMENT
- [ ] AERIAL

AQUATIC HABITATS

- ☐ GENERAL AQUATIC
- ☐ FRESHWATER
  - ☐ Wetlands/Bogs/Swamps
  - ☑ Lakes/Ponds
  - ☐ Rivers/Streams
  - ☐ Reservoirs
- ☐ MARINE
  - ☐ Open Ocean/Continental Shelf
  - ☐ Bathyal
  - ☐ Abyssal
  - ☐ Estuarine
  - ☐ Intertidal/Tidal/Coastal
  - ☐ Coral Reef
  - ☐ HYPERSALINE
- ☐ EXTREME AQUATIC ENVIRONMENT
- ☐ CAVES/ ROCK OUTCROPS/ CLIFFS
- ☐ MANGROVES
- ☐ SUBSURFACE WATERS/ SPRINGS
- ☐ EPHEMERAL POOLS & STREAMS
- ☐ MICROPOOLS (Pitcher Plants, Tree Holes, Other)

MAN-MADE ENVIRONMENTS

- ☑ LABORATORY
- ☐ THEORETICAL SYSTEMS
- ☐ OTHER ARTIFICIAL SYSTEMS

NOT APPLICABLE

- ☐ NOT APPLICABLE

CATEGORY VI: GEOGRAPHIC AREA OF THE RESEARCH (Select 1 to 2)

- ☐ WORLDWIDE
- ☐ NORTH AMERICA
  - ☑ United States
    - ☐ Northeast US (CT, MA, ME, NH, NJ, NY, PA, RI, VT)
    - ☐ Northcentral US (IA, IL, IN, MI, MN, ND, NE, OH, SD, WI)
    - ☐ Northwest US (ID, MT, OR, WA, WY)
    - ☐ Southeast US (DC, DE, FL, GA, MD, NC, SC, WV, VA)
    - ☐ Southcentral US (AL, AR, KS, KY, LA, MO, MS, OK, TN, TX)
    - ☐ Southwest US (AZ, CA, CO, NM, NV, UT)
    - ☐ Alaska
    - ☐ Hawaii
    - ☐ Puerto Rico
  - ☐ Canada
  - ☐ Mexico
- ☐ CENTRAL AMERICA (Mainland)
  - ☐ Caribbean Islands
  - ☐ Bermuda/Bahamas
- ☐ SOUTH AMERICA
  - ☐ Eastern South America (Guyana, Fr. Guiana, Suriname, Brazil)
  - ☐ Northern South America (Colombia, Venezuela)
  - ☐ Southern South America (Chile, Argentina, Uruguay, Paraguay)
  - ☐ Western South America (Ecuador, Peru, Bolivia)
- ☐ EUROPE
  - ☐ Eastern Europe
  - ☐ Russia
  - ☐ Scandinavia
  - ☐ Western Europe
- ☐ ASIA
  - ☐ Central Asia
  - ☐ Far East
  - ☐ Middle East
  - ☐ Siberia
  - ☐ South Asia
  - ☐ Southeast Asia
- ☐ AFRICA
  - ☐ North Africa
  - ☐ African South of the Sahara
    - ☐ East Africa
    - ☐ Madagascar
    - ☐ South Africa
    - ☐ West Africa
- ☐ AUSTRALASIA
  - ☐ Australia
  - ☐ New Zealand
  - ☐ Pacific Islands
- ☐ ANTARCTICA
- ☐ ARCTIC
- ☐ ATLANTIC OCEAN
- ☐ PACIFIC OCEAN
- ☐ INDIAN OCEAN
- ☐ OTHER REGIONS (Not defined)
- ☐ NOT APPLICABLE

CATEGORY VII: CLASSIFICATION OF ORGANISMS (Select 1 to 4)

- ☐ VIRUSES
  - ☐ Bacterial
  - ☐ Plant
  - ☐ Animal
- ☐ PROKARYOTES
  - ☐ Archaea
  - ☐ Cyanobacteria
  - ☐ Bacteria
  - ☐ Noncultured Organisms
- ☐ PROTISTA (PROTOZOA)
  - ☐ Amoebae
  - ☐ Apicomplexa
  - ☐ Ciliophora
  - ☐ Flagellates
  - ☐ Foraminifera
  - ☐ Microspora
  - ☐ Radiolaria
- ☐ FUNGI
  - ☐ Ascomycota
  - ☐ Basidiomycota
  - ☐ Chytridiomycota
  - ☐ Mitosporic Fungi
  - ☐ Oomycota
  - ☐ Zygomycota
- ☐ LICHENS
- ☐ SLIME MOLDS
- ☑ ALGAE
  - ☐ Bacillariophyta (Diatoms)
  - ☐ Charophyta
  - ☐ Chlorophyta
  - ☐ Chrysophyta
  - ☐ Dinoflagellata
  - ☐ Euglenoids
  - ☐ Phaeophyta
  - ☐ Rhodophyta
- ☐ PLANTS
  - ☐ NON-VASCULAR PLANTS
    - ☐ BRYOPHYTA
      - ☐ Anthocerotae (Hornworts)
      - ☐ Hepaticae (Liverworts)
      - ☐ Musci (Mosses)
  - ☐ VASCULAR PLANTS
    - ☐ FERNS & FERN ALLIES
    - ☐ GYMNOSPERMS
      - ☐ Coniferales (Conifers)

- ☐ Cycadales (Cycads)
- ☐ Ginkgoales (Ginkgo)
- ☐ Gnetales (Gnetophytes)
- ☐ ANGIOSPERMS
- ☐ Monocots
- ☐ Arecaceae (Palmae)
- ☐ Cyperaceae
- ☐ Liliaceae
- ☐ Orchidaceae
- ☐ Poaceae (Graminae)
- ☐ Dicots
- ☐ Apiaceae (Umbelliferae)
- ☐ Asteraceae (Compositae)
- ☐ Brassicaceae (Cruciferae)
- ☐ Fabaceae (Leguminosae)
- ☐ Lamiaceae (Labiatae)
- ☐ Rosaceae
- ☐ Solanaceae

☐ ANIMALS

- ☐ INVERTEBRATES
- ☐ MESOZOA/PLACOZOA
- ☐ PORIFERA (Sponges)
- ☐ CNIDARIA
- ☐ Hydrozoa (Hydra, etc.)
- ☐ Scyphozoa (Jellyfish)
- ☐ Anthozoa (Corals, Sea Anemones)
- ☐ CTENOPHORA (Comb Jellies)
- ☐ PLATYHELMINTHES (Flatworms)
- ☐ Turbellaria (Planarians)
- ☐ Trematoda (Flukes)
- ☐ Cestoda (Tapeworms)
- ☐ Monogenea (Flukes)
- ☐ GNATHOSTOMULIDA
- ☐ NEMERTINEA (Rynchocoela) (Ribbon Worms)
- ☐ ENTOPROCTA (Bryozoa) (Plant-like Animals)
- ☐ ASCHELMINTHES
- ☐ Gastrotricha
- ☐ Kinorhyncha
- ☐ Loricifera
- ☐ Nematoda (Roundworms)
- ☐ Nematomorpha (Horsehair Worms)
- ☐ Rotifera (Rotatoria)
- ☐ ACANTHOCEPHALA (Spiny-headed Worms)
- ☐ PRIAPULOIDEA
- ☐ BRYOZOA (Ectoprocta) (Plant-like Animals)
- ☐ PHORONIDEA (Lophophorates)
- ☐ BRACHIOPODA (Lamp Shells)
- ☐ MOLLUSCA
- ☐ Monoplacophora
- ☐ Aplacophora (Solenogasters)
- ☐ Polyplacophora (Chitons)
- ☐ Scaphopoda (Tooth Shells)
- ☐ Gastropoda (Snails, Slugs, Limpets)
- ☐ Pelecypoda (Bivalvia) (Clams, Mussels, Oysters, Scallops)
- ☐ Cephalopoda (Squid, Octopus, Nautilus)
- ☐ ANNELIDA (Segmented Worms)
- ☐ Polychaeta (Parapodial Worms)
- ☐ Oligochaeta (Earthworms)
- ☐ Hirudinida (Leeches)
- ☐ POGONOPHORA (Beard Worms)
- ☐ SIPUNCULOIDEA (Peanut Worms)
- ☐ ECHIUROIDEA (Spoon Worms)
- ☐ ARTHROPODA
- ☐ Cheliceriformes
- ☐ Merostomata (Horseshoe Crabs)
- ☐ Pycnogonida (Sea Spiders)
- ☐ Scorpionida (Scorpions)
- ☐ Araneae (True Spiders)
- ☐ Pseudoscorpionida (Pseudoscorpions)
- ☐ Acarina (Free-living Mites)
- ☐ Parasitiformes (Parasitic Ticks & Mites)
- ☑ Crustacea
- ☐ Branchiopoda (Fairy Shrimp, Water Flea)
- ☐ Ostracoda (Sea Lice)
- ☐ Copepoda
- ☐ Cirripedia (Barnacles)
- ☐ Amphipoda (Skeleton Shrimp, Whale Lice, Freshwater Shrimp)
- ☐ Isopoda (Wood Lice, Pillbugs)
- ☐ Decapoda (Lobster, Crayfish, Crabs, Shrimp)
- ☐ Hexapoda (Insecta) (Insects)
- ☐ Apterygota (Springtails, Silverfish, etc.)
- ☐ Odonata (Dragonflies, Damselflies)
- ☐ Ephemeroptera (Mayflies)
- ☐ Orthoptera (Grasshoppers, Crickets)
- ☐ Dictyoptera (Cockroaches, Mantids, Phasmids)
- ☐ Isoptera (Termites)
- ☐ Plecoptera (Stoneflies)
- ☐ Phthiraptera (Mallophaga & Anoplura) (Lice)
- ☐ Hemiptera (including Heteroptera) (True Bugs)
- ☐ Homoptera (Cicadas, Scale Insects, Leafhoppers)
- ☐ Thysanoptera (Thrips)
- ☐ Neuroptera (Lacewings, Dobsonflies, Snakeflies)
- ☐ Trichoptera (Caddisflies)
- ☐ Lepidoptera (Moths, Butterflies)
- ☐ Diptera (Flies, Mosquitoes)
- ☐ Siphonaptera (Fleas)
- ☐ Coleoptera (Beetles)
- ☐ Hymenoptera (Ants, Bees, Wasps, Sawflies)
- ☐ Chilopoda (Centipedes)
- ☐ Diplopoda (Millipedes)
- ☐ Pauropoda
- ☐ Symphyta (Symphyla)
- ☐ PENTASTOMIDA (Linguatulida) (Tongue Worms)
- ☐ TARDIGRADA (Tardigrades, Water Bears)
- ☐ ONYCHOPHORA (Peripatus)
- ☐ CHAETOGNATHA (Arrow Worms)
- ☐ ECHINODERMATA
- ☐ Crinoidea (Sea Lilies, Feather Stars)
- ☐ Asteroidea (Starfish, Sea Stars)
- ☐ Ophiuroidea (Brittle Stars, Serpent Stars)
- ☐ Echinoidea (Sea Urchins, Sand Dollars)
- ☐ Holothuroidea (Sea Cucumbers)
- ☐ HEMICHORDATA (Acorn Worms, Pterobranchs)
- ☐ UROCHORDATA (Tunicata) (Tunicates, Sea Squirts, Salps, Ascideans)
- ☐ CEPHALOCHORDATA (Amphioxus/Lancelet)
- ☐ VERTEBRATES
- ☐ AGNATHA (Hagfish, Lamprey)
- ☐ FISHES
- ☐ Chondrichthyes (Cartilaginous Fishes) (Sharks, Rays, Ratfish)
- ☐ Osteichthyes (Bony Fishes)
- ☐ AMPHIBIA
- ☐ Anura (Frogs, Toads)
- ☐ Urodela (Salamanders, Newts)
- ☐ Gymnophiona (Apoda) (Caecilians)
- ☐ REPTILIA
- ☐ Chelonia (Turtles, Tortoises)
- ☐ Serpentes (Snakes)
- ☐ Sauria (Lizards)
- ☐ Crocodylia (Crocodilians)
- ☐ AVES (Birds)
- ☐ Passeriformes (Passerines)
- ☐ MAMMALIA
- ☐ Monotremata (Platypus, Echidna)
- ☐ Marsupalia (Marsupials)
- ☐ Eutheria (Placentals)
- ☐ Insectivora (Hedgehogs, Moles, Shrews, Tenrec, etc.)
- ☐ Chiroptera (Bats)
- ☐ Primates
- ☐ Humans
- ☐ Rodentia
- ☐ Lagomorphs (Rabbits, Hares, Pikas)
- ☐ Carnivora (Bears, Canids, Felids, Mustelids, Viverrids, Hyena, Procyonids)
- ☐ Perissodactyla (Odd-toed Ungulates) (Horses, Rhinos, Tapirs, etc.)

☐ Artiodactyla (Even-toed Ungulates) (Cattle, Sheep, Deer, Pigs, etc.) ☐ Marine Mammals (Seals, Walrus, Whales, Otters, Dolphins, Porpoises)	☐ TRANSGENIC ORGANISMS ☐ FOSSIL OR EXTINCT ORGANISMS	☐ NO ORGANISMS

CATEGORY VIII: MODEL ORGANISM (Select ONE)

☑ NO MODEL ORGANISM MODEL ORGANISM (Choose from the list)	☐ Escherichia coli ☐ Mouse-Ear Cress (Arabidopsis thaliana)	☐ Fruitfly (Drosophila melanogaster)

PROJECT SUMMARY

Overview. The objective of the proposed research is to better link the biological mechanisms that promote species coexistence to the ecological functioning of communities. Throughout most of the history of community ecology, it has been assumed that niche differentiation among species is the sole biological mechanism that offsets the negative effects of interspecific competition and prevents competitive exclusion. But theories of species coexistence have undergone a major revision recently, and we now know there are two forces that jointly regulate species interactions and coexistence in competitive communities. Niche differences (NDs) stabilize species interactions and facilitate coexistence, whereas relative fitness differences (RFDs) establish competitive hierarchies that promote competitive exclusion. Theory predicts that ND's must be sufficiently large to offset and stabilize the competitive hierarchies generated by RFD's; however, I know of few empirical tests that show how these two forces jointly influence coexistence in real communities. And to my knowledge, there has yet to be any assessment of how ND/RFD influence the ecological functions performed by species assemblages.

I will test two hypotheses about how ND and RFD jointly regulate species coexistence and the production of biomass in multi-species assemblages.

Hyp 1. ND must exceed RFD by the minimum $[1 - ND]^{-1} > RFD$ *in order for species to coexist.*
Hyp 2. Biomass production in any mixed species assemblage is proportional to ND – RFD.

Using freshwater algae as model system, I will test these hypotheses with a set of experiments performed in laboratory chemostats where I can achieve the high level of replication and control needed to interpret how ND and RFD influence the coexistence and productivity of many algal species combinations. To complement interpretation of the lab work, I will examine whether measures of ND and RFD predict patterns of co-occurrence of species combinations in natural lakes across the continental U.S. Lastly, I will complete a set of field experiments where I will reciprocally transplant algal assemblages from natural ponds into mesocosms to measure mutual invasibility and ecological function. Freshwater algae are a good model for the proposed work because they have been used in the development of several prior theories about competition and coexistence, and because my lab has pioneered methods for quantifying ND and RFD using these organisms.

Intellectual merit. The primary intellectual merit of this work will be to forge a better link between the causes and consequences of species coexistence. Many fields of ecology (e.g., *ecological stoichiometry*, *ecosystem engineering*, *biodiversity and ecosystem functioning*) have bridged ideas from community and ecosystem ecology by looking at how species interactions and the mechanisms that drive coexistence influence the ecological functions performed by individual species or by biodiversity. But work in these fields have rarely used modern theories of species coexistence to determine how the balance of opposing forces (ND and RFD) influence coexistence and the functions performed by species. The work proposed here is an important step towards understanding how the balance of forces that control the outcome of species interactions simultaneously influence the ecological functions performed by species in communities.

Broader impacts. This proposal includes several broader impact activities that build on programs established with prior NSF support, and which have demonstrated histories of success. First, I will partner with a local nonprofit organization (the Leslie Science & Nature Center) that provides environmental education to >25,000 K-12 students annually. My students, postdocs and I will organize and lead two *'Aquatic Scientist'* summer camps per year for 120 3rd to 6th graders. Second, I propose two programs to broaden participation in STEM. One will take place with the Univ. of Michigan's Center for Engineering Diversity and Outreach to provide summer research internships for 12th grade students from under-represented groups. A second will occur by working with U-M's Doris Duke Scholars Program to provide summer internships to undergraduates selected to introduce greater diversity into the environmental conservation workforce. These broader impacts will not only give students research experience in aquatic sciences, they will provide the guidance needed to prepare for college and persist in achieving a university STEM degree.

TABLE OF CONTENTS

For font size and page formatting specifications, see GPG section II.B.2.

Appendix Items:

*Proposers may select any numbering mechanism for the proposal. The entire proposal however, must be paginated. Complete both columns only if the proposal is numbered consecutively.

RESPONSE TO PRE-PROPOSAL REVIEWS

Scores for this pre-proposal were Excellent, Excellent/Very Good, and Very Good. The panel said it was *'enthusiastic about the proposed research and its potential to provide a strong test of new coexistence theory.'* Individual panelists commented that:

- *The proposal is well vetted in ecological theory and aims to further advance our understanding of mechanisms that promote coexistence and community function.*
- *The proposed chemostat & common garden experiments constitute a strong experimental approach.*
- *This is elegant work that tests fundamental ideas in coexistence theory in a proven system. It's hard to find much to criticize and the work should add substantially to our knowledge of coexistence.*

Despite generous remarks, reviewers did, in fact, make several suggestions. One was that the proposed experiments focused too heavily on resource partitioning as the primary axis of niche partitioning among algal species. Based on panel suggestions, I expanded the experiments to also consider niche axes generated by shared grazers. And while reviewers liked that the broader impacts I proposed built on a strong track record of outreach and mentoring programs established during prior grants, they did ask me to clarify what new impacts would be established, and how those would be integrated with this grant. In response, I offer more detail about how this grant will advance my long-standing education and outreach programs.

INTRODUCTION

<u>The objective of the proposed work is to better link the biological mechanisms that promote species coexistence to the functioning of ecosystems</u>. Using freshwater algae as a model system, I will test two new hypotheses about how the two forces that moderate species interactions in modern models of coexistence – niche and relative fitness differences – jointly regulate species coexistence and the production of biomass in multi-species assemblages.

Background

<u>Historically, it's all been about niches</u>. Throughout most of the history of community ecology, it has been assumed that niche differentiation among species is the sole biological mechanism that can offset the negative impacts of interspecific competition and prevent competitive exclusion[1-8]. This idea dates at least to 1928 when Volterra[1] introduced a dynamic model of competition that became the foundation for the competitive exclusion principle[2]. The competitive exclusion principle led to the conclusion that ecosystems should only contain as many species as there are limiting resources (or consumers); thus, species only coexist if they use different limiting resources (consumers) at the same location and time, or if they partition resources (consumers) in space or time[8-12]. Nearly all subsequent hypotheses to explain coexistence have argued that biodiversity exists because of niche differences among species.

<u>Modern theory says that coexistence is driven by more than just niches.</u> While niche partitioning has been the foundation for most explanations of the world's biodiversity, theories of species coexistence have recently undergone a major revision. In 2001, Hubbell published *The Unified Neutral Theory of Biodiversity*[13], which argued that patterns of biodiversity in nature can be explained by a relatively simple model that does not invoke niche differences among species. According to Hubbell's theory, species coexist not because they are different, but because their demographic parameters are identical and the consequences of their interactions are 'neutral' (i.e. equal among all species). As such, Hubbell argued that the biodiversity we observe in nature can be explained by a series of stochastic events that give some populations the chance opportunity to rise to dominance while others exhibit random walks to extinction.

While Hubbell was developing neutral theory, Chesson[14] was completing a ground-breaking synthesis of coexistence theory that would ultimately provide a road map for how to integrate niche and neutral perspectives on biodiversity. Chesson showed that coexistence in most mathematical models of competition is simultaneously controlled by two forces, which he called *stabilizing* and *equalizing*. Stabilizing forces represent various forms of niche differentiation (ND), all of which cause species to limit their own growth more strongly than they limit the growth of other species (intra > interspecific competition). This can occur when species partition limited resources in space or time, or when they experience differential consumption by shared consumers. In contrast, equalizing forces minimize what Chesson and others now refer to as relative fitness differences (RFD) among species[15-18]. Chesson's definition of a 'fitness difference' is not the same as that used by evolutionary biologists, as he was referring to differences in competitive abilities among species, not fitness differences among individuals. RFDs set up competitive hierarchies among species, and are the result of inherent variation in biological traits such as minimum resource or consumer requirements (R*/P*'s), differential resistance to consumers, or differences in growth rates[15-17]. RFDs represent differences in competitive abilities that persist irrespective of how much ND there are among species.

Importantly, Chesson showed it is the balance of these two forces – RFDs that establish competitive hierarchies, and NDs that prevent competitive exclusion - that ultimately determine whether species maintain positive long-term growth rates in competitive communities[14]. To coexist, ND must be sufficiently large to offset and stabilize the competitive hierarchies generated by RFD's. It has subsequently been shown that Hubbell's neutral theory represents a very specific, limiting case of Chesson's coexistence theory where NDs and RFDs are both zero, causing the outcome of competition to be approximated by a random walk to extinction[15]. Thus, Chesson's framework is a more general approach for understanding species coexistence.

To date, studies of how species function in communities have considered only half of coexistence theory. While modern coexistence theory was undergoing a major revision, a separate body of work was examining how species interactions and niche differences influence the productivity of communities. From 1995 to 2010, more than 500 experiments were completed in which researchers grew species of plants or algae alone in monoculture, and together in mixed-species polycultures[19-26] to look at how interactions among species affect the 'functioning' of communities. Meta-analyses of these studies have shown that mixed-species assemblages generally produce more biomass than the average of their component species and, in roughly 33% of cases, they produce more biomass than their highest yielding species[22,27]. The most common explanation for these results is that niche differences among species reduce inter- relative to intraspecific competition and allow species mixtures to more fully exploit available resources[28-30]. But not only are niche differences rarely measured directly in these studies[22], nearly all of this work has assumed that competition and coexistence are solely the product of ND. I know of no study that has measured how both of the forces that comprise modern models of coexistence (ND and RFD) jointly regulate species coexistence and, in turn, affect the ecological functions performed by species in mixed assemblages.

Objective

It is prime time to quantify how ND and RFD jointly influence species coexistence and ecological function*.* I believe the field of community ecology is at a point that is similar to where evolutionary biology was in the 1930's when numerous sub-disciplines in biology began to forge a common view of processes that control evolution (referred to as the Modern Evolutionary Synthesis[31]). During this period, the rediscovery of Mendelian inheritance[32] and formation of the chromosomal theory of inheritance[33] revealed the units of evolution (genes) to match the mechanism of evolution (natural selection) described by Darwin in the previous century[34]. Our understanding of evolution was then complemented by Kimura's *Neutral Theory of Molecular Evolution*[35,36], which argued that the frequency of alleles in nature is not just due to natural selection, but is also the product of genetic drift of mutant alleles that are neutral.

Similarly, ecologists since the time of Volterra[1] and Gause[2] have spent much of the last century working to explain the biological mechanisms and functional traits that underlie niche differences that control species coexistence. Our understanding of coexistence was complimented by Hubbell[13] who proposed that species diversity in nature is also influenced by the stochastic drift of species whose interactions are neutral. Chesson[14] then provided the insight needed to forge a common view of processes that influence coexistence when he showed that nearly all models of competition have elements of both the niche and neutral perspectives, but that two forces (niche and relative fitness differences) operate simultaneously to maintain species coexistence. Now that we have Chesson's conceptual and mathematical synthesis, community ecology is, for the first time, in position to quantify the joint influence of these two forces in maintaining species richness in communities, and to understand how the mechanisms of coexistence influence the ecological functions performed by species when together in an assemblage.

STUDY SYSTEM AND GENERAL APPROACH

I will use freshwater algae as a model system to test two new hypotheses about how niche differences (ND) and relative fitness differences (RFD) influence species coexistence and biomass production in mixed-species assemblages. Freshwater algae are a good study system because:

Models of competition. Ever since Hutchinson posed the paradox of the plankton[37], freshwater algae have served as models for the development of numerous theories and mathematical models of competition and coexistence[38-46]. One reason they serve as a good model system is that their rapid generation times allow one to characterize the population dynamics needed to quantify species interactions and test for long-term coexistence.

Readily measureable 'functions'. Photosynthesis and biomass production are measures of ecological function that can be readily quantified for primary producers in aquatic systems.

Ecological importance. More than 50% of phytoplankton biomass production in aquatic systems is consumed by herbivores (3x greater than in terrestrial systems)[47,48], highlighting the essential role phytoplankton play in maintaining higher trophic levels in freshwater.

Methods to measure ND and RFD. Lastly, and perhaps most important, freshwater algae are one of the few study systems in which we've already learned how to quantify niche and relative fitness differences (Box 1). I am only aware of two methods that have been developed to measure ND and RFD in real communities. One is quantification of *negative frequency dependence* (also called *advantage when rare*), which has been used by terrestrial plant biologists[15-17]. The magnitude of negative frequency dependence is a measure of the strength of ND among species, and is quantified as the change in a species per capita growth rate when that species is rare vs. common in a community. Because rarity can be experimentally manipulated, Levine and Hille Ris Lambers[17] have shown that one can remove ND among species and then measure the residual impacts of RFD on competition in the absence of any ND.

The second way to measure ND and RFD in real communities is by quantifying *mutual invasibility*. This is the approach my research group has helped pioneer using freshwater algae[49-52]. Box 1 illustrates how *mutual invasibility* is measured experimentally for a hypothetical system of two species, and then used to calculate ND and RFD for a species pair. Briefly, each of two species are grown alone as monocultures to quantify their per capita growth rates in the absence of interspecific competition, $\mu_{i,mono}$. Each is then introduced at low density as invaders into steady-state populations of their potential competitor. The proportional reduction in a species per capita growth rate when introduced as an invader, $\mu_{i,inv}$, verses when grown alone, $\mu_{i,mono,}$ is a measure of how sensitive the species is to competition with the other species ($S_i = [\mu_{i,mono} - \mu_{i,inv})/ \mu_{i,mono}]$). If sensitivities are large ($S_i \rightarrow 1$), then we assume species have strongly overlapping niches that lead to strong competition. If sensitivities are small ($S_i \rightarrow 0$), we assume species are fully niche differentiated, and therefore, there is no competition that leads to a reduction in growth rate. The geometric mean of species sensitivities to competition represents the amount competition among species, which is proportional to 1 - ND. Variation around the mean represents relative fitness differences that generate competitive hierarchies. Even if ND = 0, RFD can still be > 0 and generate dominance by one species over the other.

Box 1: Quantifying niche and relative fitness differences. Researchers have developed two ways to measure ND and RFD in real communities: quantification of (1) negative frequency dependence, and (2) mutual invasibility. Narwani et al.[53] showed mathematically that these methods are interchangeable. I plan to use *mutual invisibility* for work proposed here, and Fig. 1 illustrates how it is quantified experimentally for a hypothetical system of two species. Species A (blue) and B (red) are grown alone in monoculture where population densities are sampled through time to estimate per capita growth rates ($\mu_{i,mono}$). Species A is then introduced at low density into a culture of B that has been grown to steady state, and vice versa. The sensitivity of each species to competition (S_i) is then quantified as the proportional reduction in per capita growth rates (μ_i) when invading a steady-state population of a potential competitor relative to the growth rate achieved when alone in monoculture, $S_i = (\mu_{i,mono} - \mu_{i,inv})/\mu_{i,mono}$. Coexistence occurs when species populations are mutually invasible (intra- > interspecific competition when all $S_i < 1$).

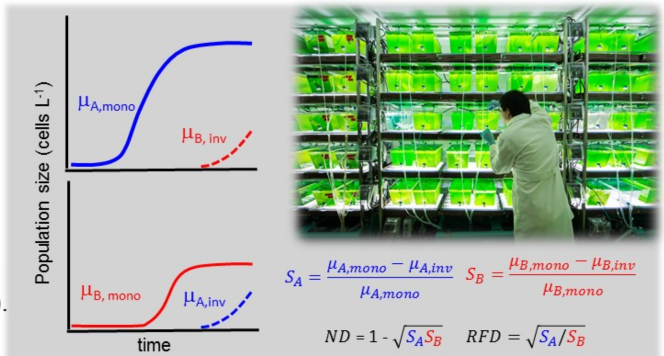


Fig 1. Illustration of the design of a mutual invasibility experiment involving 2 species.

Carroll et al.[51] showed that ND can be quantified as the geometric mean of the S_i's, $ND = 1 - \prod_{i=1}^{n} S_i^{1/n}$,which is $1 - \sqrt{S_A S_B}$. for n = 2 species. RFD is the std. deviation of the geometric mean, $RFD = \exp(\sqrt{(\sum_{i=1}^{n}\left(\ln\frac{S_i}{ND}\right)^2)/n}$, or $\sqrt{S_A/S_B}$ for n = 2. Greater ND reduce the sensitivity of both species' to competition, whereas greater RFD cause species to be asymmetrically affected by competition such that one species S_i increases while the other decreases. It is important to note that ND and RFD are properties of a community, not of individual species. While they quantify the amount of niche differentiation and strength of competitive hierarchies among all species in a community, they do not tell us how species differ in resource or consumer requirements, nor what makes one species superior to another. To address these questions, additional information on biological traits that underlie competition or consumption are required.

HYPOTHESES

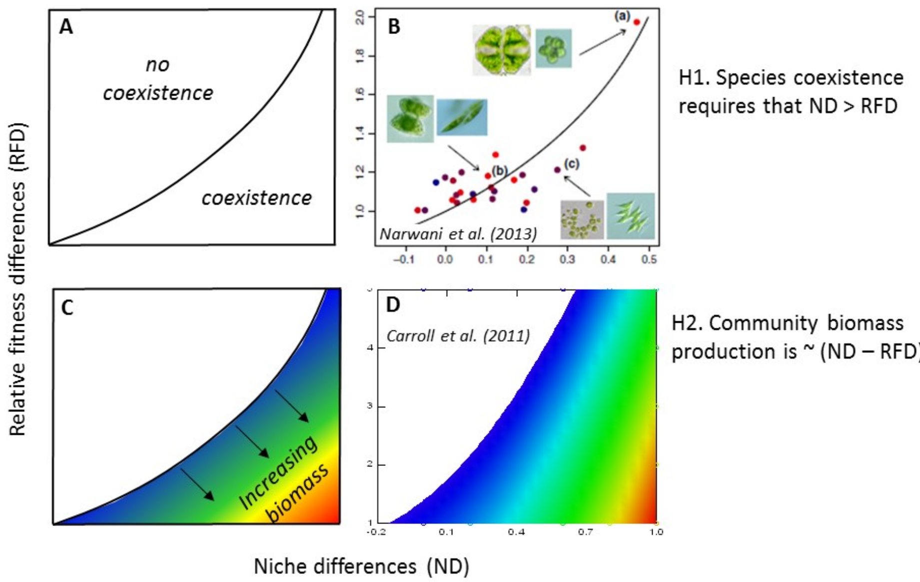
I will use the mutual invasibility criterion to test two novel hypotheses about how niche differences (ND) and relative fitness differences (RFD) influence species coexistence and biomass production in mixed-species assemblages.

<u>Hypothesis 1. Species coexistence requires that niche differences (ND) exceed relative fitness differences (RFD) (Fig 2A).</u> Modern theory predicts that species coexistence is influenced by the balance of ND and RFD, and goes on to suggest that ND must exceed RFD by the minimum $[1 - ND]^{-1} > RFD$[51,53]. Biologically speaking, this inequality represents the point at which the per capita growth advantage of species being 'different' from one another exceeds the per capita disadvantage of the competitive hierarchy on growth of the inferior species. To date, few tests of H1 exist (but see[17]) and I know of no attempts to quantify minimum thresholds of coexistence. My lab is one of the few that has been able to quantify ND and RFD to look at their joint influence on the coexistence of freshwater algae. Using the *mutual invasibility* criterion (Box 1), my postdocs and I have quantified the sensitivities of select algal species to competition when invading steady-state populations of one another, and used those to estimate ND and RFD[53]. We have found that some species combinations exhibit large ND, but still do not coexist because they also have large RFD that generate large competitive hierarchies (Fig. 2B, point a). Other combinations have very small ND's, but still coexist because their RFDs are correspondingly small (Fig. 2B, point b). While our pilot studies are consistent with H1, work so far has been limited to just a handful of species interacting in small (1-mL) well-plates. The studies detailed in the proposal will test H1 by quantifying ND and RFD using far better lab-based, and more realistic field-based studies that involve a much broader range of freshwater algae.

<u>Hypothesis 2. The production of community biomass is proportional to the difference ND – RFD (Fig 2C).</u> To my knowledge, no empirical work has examined how ND and RFD jointly influence

ecological processes such as biomass production. However, my lab has developed H2 theoretically[51] showing that ND and RFD jointly regulate the biomass yield of any mixed species assemblage in MacArthur's[12] classic model of exploitative competition (Fig. 2D). When ND are only slightly larger than RFD, species coexist but don't produce any more biomass than the competitively superior species, which dominates the community. When ND are much larger than RFD, species coexist and the small competitive hierarchies ensure that species abundances are more even, ensuring greater complementary use of resources and more biomass production. Although niche partitioning has long been perceived as the primary mechanism that increases community biomass[28,30,54,55], our work predicts that reducing RFD can have equally large impacts on ecological functions.

Fig 2. Hypotheses & preliminary data. H1, which proposes that species only coexist when ND exceed RFD (panel A), was supported by Narwani et al. (Ecol Lett 2013)[53] who measured mutual invasibility of 8 algal species and found that, despite strong ND, invasibility only occurred in combinations where ND > RFD (panel B). H2, which proposes that community biomass increases as ND grow large relative to RFD (panel C), was supported by Carroll et al. (Ecology 2011)[51] who separated the influence of ND and RFD on biomass production in mono- and polycultures using MacArthur's classic model of competition[10].



PROPOSED RESEARCH

I will test Hypotheses 1 and 2 with a complimentary set of lab-based and field-based studies. The first study will involve a set of experiments performed in laboratory chemostats where I can achieve the high level of replication and control needed to interpret how ND and RFD influence the mutual invasibility, coexistence, and productivity of many algal species combinations. To complement interpretation of the lab work, I will examine whether measures of ND and RFD predict patterns of co-occurrence of species combinations in natural lakes across the continental U.S. using the Environmental Protection Agency's National Lakes Assessment. The second study will involve a set of field experiments where I will reciprocally transplant algal assemblages from natural ponds into mesocosms to measure mutual invasibility and ecological function. All three reviewers of the pre-proposal commented that the close tie between lab and field work was a key strength of the proposal. However, referees asked me to expand the experiments to consider not only partitioning of inorganic resources as a mechanism of coexistence, but also niche axes generated by shared grazers. I have taken their suggestion, and significantly expanded the size of the experiments to include grazer treatments.

Study 1. Mutual invasibility lab experiments (years 1-2)
This study will use the *mutual invasibility* criterion (Box 1) to quantify how ND and RFD influence the probability of coexistence and production of biomass for 60 combinations of algae grown in laboratory chemostats. Results will be 'ground-truthed' by examining whether ND and RFD can also

help explain patterns of co-occurrence of each species combination in natural lake ecosystems across the continental U.S.

Focal species. As part of my prior DIMENSIONS of Biodiversity grant (see *Results of Prior NSF Support*), I established cultures of 55 freshwater green algae (Chlorophyta and Charophyta) that represent some of the most widespread and abundant species throughout N. American lakes (based on the U.S. EPA's 2007 National Lakes Assessment of 1,028 lakes). During this grant my lab group (1) produced a highly resolved molecular phylogeny describing evolutionary relationships among green algae[56], (2) performed lab experiments to determine if evolutionary relatedness predicts the strength of species interactions[50,57], (3) examined whether phylogenetic diversity can explain patterns of species co-occurrence in lakes across the U.S.[53,56], and (4) quantified species functional traits, including morphological (body size, shape) and demographic (intrinsic growth rates) traits, as well physiological traits like the dependence on growth rates of nutrients (N, P) and light to determine which traits are phylogenetically conserved[49,58]. While this work gave us much information on competition and coexistence in green algae, I did not test the hypotheses in this proposal about how ND/RFD influence species coexistence and ecological function.

The lab experiments proposed here will focus on a subset of 12 species that I've used in my prior studies (*Ankistrodesmus falcatus, Botryococcus sudeticus, Chlorella sorokiniana, Coelastrum microporum, Crucigenia tetrapedia, Monoraphidium minutum, Oocystis parva, Oocystis polymorpha, Pediastrum boryanum, Pediastrum tetras, Scenedesmus acuminatus, Selenastrum capricornutum*). In past experiments[53,59,60], combinations of these species have represented the full range of competitive interactions - from complete dominance to weak interactions, as well as wide variation in ND and RFD (see Fig. 2B for an example, and Fig. F2 in *Facilities, Equipment and Other Resources* for preliminary data on these particular species).

The lab-based experiments described below will also utilize the cladoceran grazer *Daphnia pulex*, which is globally distributed[61]. This zooplankter co-occurs with the focal algae chosen for this study in ca. 30% of lakes throughout N. America (based on the 2007 EPA National Lakes Assessment). Numerous studies have shown that *D. pulex* exhibits differential consumption of various species of algae[62-64]. My own lab's work suggests that *D. pulex* feeds preferentially on larger species of green algae that tend to be competitively dominant for inorganic resources[65]. This suggests a trade-off may exist between the competitive abilities of algal species verses their susceptibility to grazing by *D. pulex*. Such trade-offs are a signature of niche partitioning generated by shared grazers[14,66,67], and their potential to moderate algal coexistence via life-history trade-offs is the primary reason I have selected *D. pulex* as the focal consumer for this study.

Experimental design. With 12 species of algae in the species pool, there are 66 possible two-species combinations. From these, I will quantify *mutual invasibility* for 45 combinations (68%) - a number chosen because it is the upper limit of experimental units available. Experimental units will be 9.5-L chemostats that were specifically designed for long-term culture of algae (see *Facilities, Equipment, and Other Resources*). My lab's experimental facility at the University of Michigan has 180 chemostats housed on 6 racks (30 chemostats rack^{-1}). Growth media to the chemostats is delivered automatically from holding tanks that sit below the rack and maintain H_2O temperatures at 20 C°. Lighting beneath the chemostats consists of five T5 fluorescent lamps that emit full spectrum light at 450 μE m^{-2} sec^{-1}, which is sufficient to saturate algal growth. For this experiment, I will use COMBO growth media exchanged at 10% per day, and modified to have an N:P ratio comparable to the median of the species pool to maximize the chance of limitation by more than one nutrient (see cell stoichiometries, Table F1 of the *Facilities, Equipment and Other Resources*). COMBO is a widely used media for freshwater alga culture[68,69], and the media, exchange rate, and temperature mimic conditions used in prior experiments where my lab has quantified competition among algae[50,56,57,59].

For each combination of algae, there are two different orders of introduction (species A invading a steady-state culture of B, and vice versa). I plan to cross each combination of algae with two herbivore treatments – one a no herbivore treatment where algae will presumably compete for inorganic resources (nutrients, light), and one treatment with *D. pulex* where competition and coexistence among algae will potentially be modified by grazing.

The experiment is designed as a randomized complete block in which one replicate of each algal species combination by herbivore treatment is run in each of six temporal blocks:

45 species combinations of algae × 2 orders of introduction
× 2 herbivore treatments (no herbivores, +*D. pulex*) = 180 chemostats
× 6 experimental blocks (reps) = 1,080 total chemostats (6 replicates per treatment combination)

To begin each block of the experiment, sterilized chemostats will be filled with COMBO growth media, after which, they will be inoculated with low densities (10,000 cells mL^{-1}) of the initial algal species. I will then begin monitoring algal growth in the chemostats.

Algal growth curves. This experiment is a bit unusual in the sense that mutual invasions must occur when resident plankton have grown to steady state, as this is where one needs to measure ND/RFD and how these influence productivity. Because species range in doubling times from 1 to 4 days, it can take cultures anywhere from 10 to 40 days to reach steady state (note demographic parameters in Table F1 in *Facilities, Equipment and Other Resources*). Given this, I need a way to track the growth curves of the plankton in real time, and use these curves to guide decisions on when to start mutual invasions. To accomplish this, I will take 3 1-mL subsamples from each experimental unit on each day of the experiment and analyze them on a BioTek FLx800 microplate reader to measure in-vivo fluorescence of chlorophyll-a as a proxy for algal biomass. Though an imperfect measure of biomass, in-vivo fluorescence can be analyzed immediately and non-destructively; allowing me to get relative changes in the biomass of each experimental unit in near real-time. I will fit values of fluorescence to logistic growth curves $dF_i/dt = \mu_{i,mono} F_i (1 - F_i/Fmax_i)$ that are updated daily (ex. Fig. 3), and use these curves to ensure mutual invasibility and subsequent measurements are taken at comparable points in the growth trajectories of experimental units.

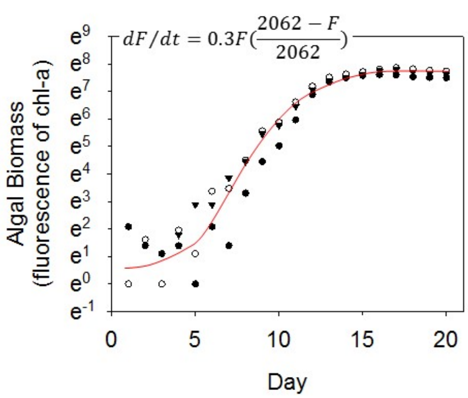


Fig 3. Algal growth curve. An example of one growth trajectory for *Ceolastrum microporum* tracked with daily measures of fluorescence. Data points represent 3 replicate cultures with parameter values estimated as maximum likelihood fits.

After measuring fluorescence, sub-samples will be combined and preserved in 3% formalin. These will later be used to estimate population sizes by counting cell densities under a microscope on a hemacytometer. Cell densities give more precise estimates of population growth than fluorescence, but take months to complete. Once complete, cell densities will be fit to exponential growth curves $dN_i/dt = \mu_{i,mono} N_i$ to quantify per capita population growth rates, $\mu_{i,mono}$, of species grown in mono-culture. Steady state cell densities of the initial species will also be measured at this time (cells L^{-1})

Mutual invasion. Once algae in a chemostat reach steady-state (when dF_i/dt is not significantly different from 0 for three successive dates, Fig. 3), the second algal species will be introduced at low density (e.g., species B will be introduced at 10,000 cells mL^{-1} into a steady-state culture of species A, and vice versa). At the same time, I will introduce the *D. pulex* into the appropriate experimental units at 33 adults L^{-1}, which falls within the range of natural densities and mimics that used in my prior studies[65]. Introducing herbivores while algae are at steady-state is essential to ensuring that all algal species – both resident, and invaders – experience consumption for an equal time period.

After introduction of herbivores and algal 'invaders', I will continue to take water samples every day to monitor fluorescence and cell densities of both algal species until fluorescence values reach a new steady-state. At that point, I will take final measurements:

- *ND and RFD.* Cell densities of the invading algal species will be fit to exponential growth curves $dN_i/dt = \mu_{i,inv}N_i$, but this time where estimates of the per capita population growth rate, $\mu_{i,inv}$, represent species invading a steady-state culture of potential competitor. Using $\mu_{i,mono}$ and $\mu_{i,inv}$, I will calculate the sensitivity of each species to competition (S_i), and niche (ND) and relative fitness differences (RFD) among the species pairs (as in Box 1).

- *Biomass yield*. The steady-state biomass yield of each species, B_i, will be estimated by multiplying steady state cell densities (cells L^{-1}) by species-specific cell biovolumes (μm^3 $cell^{-1}$) quantified via cell imaging on a Fluid Imaging Flowcam. Population level biovolumes (μm^3 L^{-1}) will be converted to biomass (μg L^{-1}) assuming a specific gravity of 1.0 (i.e. most of the cell is H_2O), after which total biomass of the assemblage is then $B_T = \sum B_i$'s.

- *Primary production*. At steady state, the rate of net biomass production in a chemostat, B_P, is equal to the standing crop biomass times the dilution rate. In addition to the net rate of biomass production, I plan to also measure instantaneous rates of gross photosynthesis to account for the potential differences in photosynthetic yields among cultures. Rates of gross photosynthesis (*GP*) will be measured by sealing chemostats to be airtight, and then measuring changes in dissolved [O_2] during light/dark incubations[70]. Community respiration (*R*) will first be determined as the decrease in $[O_2]_{dissolved}$ during a 4-hr incubation in the dark. Changes in O_2 will be measured with a PreSens laser optic probe that detects fluorescence of an oxygen sensitive 'spot' fixed to the inner surface of the chemostats. Net metabolism (*M*) will then be measured as the increase in $[O_2]_{dissolved}$ during a comparable exposure to light[70]. *GP*, which is *R* + *M*, will be standardized by biomass yields, B_T, to give the biomass specific rate of photosynthesis, *BSP*. *BSP* is the instantaneous rate of new tissue formation, and is a measure of how efficiently organisms are converting inorganic resources into biomass. I have used these methods to measure productivity in several other studies[71-77].

<u>Statistical analyses and critical tests</u>. To test H1, I will use a logit regression, $log\frac{p(x)}{1-p(x)} = \beta_0 - \beta_1(ND - RFD) + \varepsilon$, where *p(x)* is the probability of coexistence (determined as mutual invasibility for any two species, 1 = yes, 0 = no). With rare exception such as intransitives (which I have never observed in this species pool), all models for competitive communities predict that coexistence is only possible when species populations are mutually invasible at steady-state (intra- > interspecific competition when all $S_i < 1$). If H1 is supported, then I predict β_1 will be positive and *p(x)* will transition from 0 to 1 at approximately $[1 - ND]^{-1} > RFD$. To test H2, I will use a general linear model, $y = \beta_0 + \beta_1(ND - RFD) + \varepsilon$, where *y* is the log-transformed B_T, B_P, *GP*, or *BSP*. If H2 is supported, I predict β_1 will be positive.

<u>Supplemental analyses</u>. As noted in Box 1, while ND and RFD quantify the magnitude of niche differentiation and competitive hierarchies among species pairs, they do not tell us what the species compete for, or what makes one species superior to another. To understand these issues, one needs to identify biological traits that underlie species interactions, and that generate life-history trade-offs among species. The most likely axes of differentiation among species in the lab experiments are trade-offs in species abilities to compete for inorganic resources (light, N, P), or their susceptibility to grazing. I will measure four classes of functional traits that potentially regulate these trade-offs and, in turn, variation in ND/RFD among species pairs.

- *Demographic traits* that often control RFD in mathematical models of coexistence include species intrinsic rates of growth and steady-state carrying capacities. These will be measured directly in the proposed experiments.

- *Morphological traits* that influence competition for inorganic resources as well as grazer resistance include cell size (e.g., cell diameter, area, biovolume), shape (e.g., surface roughness, cell elongation, compactness), motility (e.g., presence/absence of flagella, buoyancy), and structure (formation of colonies, or spines that resist grazing).

- *Resource utilization traits* that control species abilities to compete for nutrients and/or light will be measured in supplemental experiments like those previously completed in my lab[49,78,79]. Algal species will be introduced at low densities into 1-mL well plates where light intensity is varied using neutral density filters, or where concentrations of different nutrients (NH_4, NO_3^-, PO_4^{3-}) are varied independently. The exponential growth rates of each species will then be quantified by cell counts and fit to the Monod function, $\mu = \mu_{max}R/R(\mu_{max}/\alpha)$, where μ is the average growth rate at each light intensity or nutrient concentration *R*, μ_{Max} is the maximum growth rate a species achieves at unlimited intensity/concentration, and α is the initial rate of change showing how growth rates respond at low intensity/concentration. From the Monod function I will estimate the min. requirement (*R**) for light, N, or P where μ equals zero. To compliment these measures of resource acquisition, I will quantify the tissue stoichiometry of algal species (C, N, and P) to determine elemental needs.

- *Grazer resistance traits* that control the susceptibility of algae to consumption will be measured in supplemental experiments like those my lab has performed using *D. pulex* and other cladocerans (Fig. 3 in Rakowski & Cardinale, Oikos 2016[65]). Briefly, each of the algal species is grown alone as a monoculture, and together in the 45 bicultures, both in the presence vs. absence of *D. pulex*. Species-specific susceptibility to grazing in each biculture is quantified as the ratio of algal biovolume in treatments with ($BV_{herbivore}$) versus without herbivores ($BV_{control}$).

The above functional traits have all been shown to mediate trade-offs among algae[44,80] and to influence plankton community structure[81,82]. My lab group has published numerous studies using these methods to measure algal traits and relate them to competitive abilities[45,46,49,52,55,5765,83] (see Table F1 of *Facilities, Equipment and Other Resources*). To analyze how ND and RFD are related to species traits, I will use a matrix version of a multiple regression, $Y = \beta_1 T_1 + \beta_2 T_2 \ldots \beta_k T_k + \varepsilon$ where Y is an $n \times n$ species matrix of the ND or RFD among species pairs, and T_k is an $n \times n$ species matrix with entries representing the difference in trait value k among species pairs (i.e. the difference separating species in trait 'space'). T_k entries will centered (mean = 0) and standardized (std. dev =1) to allow comparison among traits expressed in different units. I predict that traits associated with ND or RFD will have $\beta_k <> 0$.

<u>Patterns of natural co-occurrence</u>. To complement interpretation of the lab-based work and assess whether results are consistent with species composition in real lakes, I will examine the patterns of co-occurrence of each species combination in natural lake ecosystems using the U.S. Environmental Protection Agency's National Lakes Assessment (NLA) survey. This database contains algal counts for 1,157 lakes sampled 1-2× in the summer of 2007 using consistent methodologies. For the species pool used in the lab experiments, there are 637 lakes in which at least two of the taxa co-occur. From these lakes, I will determine how many times each pairwise combination of the taxa was observed in the NLA lakes on the same visit. I will then convert the number of visits into a frequency of co-occurrence by dividing the number of co-occurrences by the total number of visits. I will then use linear regression to assess whether the frequency of co-occurrence of species pairs used in the experiment can be predicted by the magnitude of ND-RFD. This analysis is identical to those my lab has previously completed to look at whether the phylogenetic distances separating species can predict patterns of co-occurrence[53,56].

<u>Limitations and future work</u>. Obviously, a study performed in laboratory chemostats has numerous limitations. Not only are the results and outcomes specific to the conditions of the chemostats themselves (type of media, dilution rates, etc.), the study will explore but a limited number of species and food-web structures, which precludes generalizations. These experiments will already cost >$250K and take nearly two years to execute. So expanding their scope in a single proposal is not feasible. But I consider this to be the first in a sequence of proposals that will link modern theories of coexistence to the functioning of communities. To prepare for future work, I will encourage postdocs, graduate students and undergraduate assistants to develop projects that are complementary to this proposal and extend consideration to other conditions, species, and trophic structures.

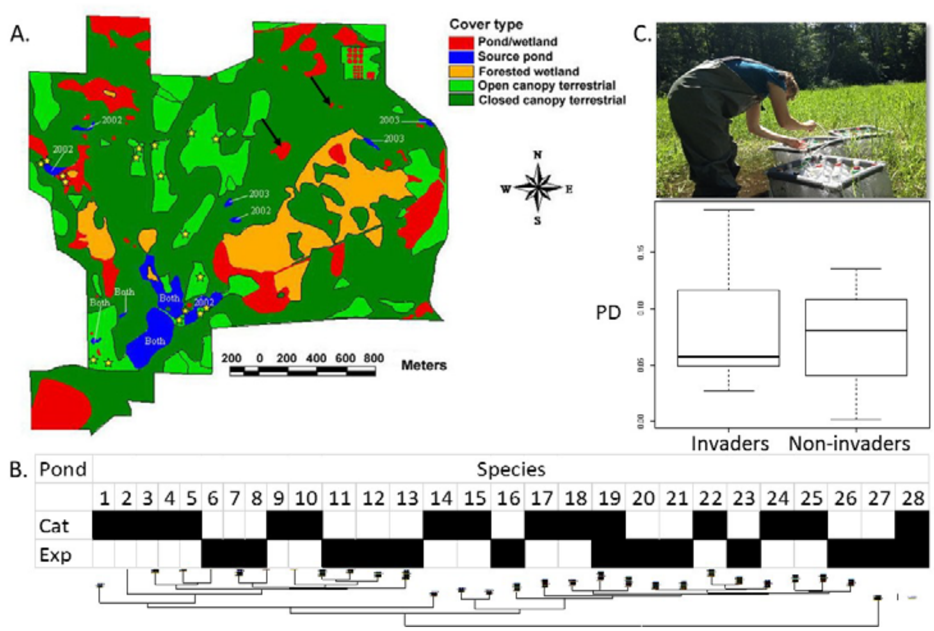
A second limitation is that the experimental units will not be axenic. In fact, for many species of algae, it is difficult if not impossible to obtain bacterial free cultures in which algae survive. I recognize the limitations of treating bacteria as a 'black box', and have already initiated a complementary research project with a postdoc who I co-fund with a microbial biologist at U-M (Dr. Vincent Denef). Together, we recently began looking at whether algae have unique bacterial associations, and whether these associations influence competitive interactions among algae. Once we have sufficient pilot data, we anticipate writing a proposal in the near future to explore how auto- / heterotroph interactions regulate coexistence and function.

Lastly, I acknowledge that chemostats do not represent the complexities of real ecosystems. I am fully aware of long-standing arguments in ecology by those who do not value lab experiments or mesocsoms as a way to advance knowledge of ecological systems[84,85]. Personally, I do not agree with those who suggest certain ways of gaining knowledge are superior to others. I believe that highly controlled lab experiments are an essential tool for testing hypotheses that often cannot be 'cleanly' tested in a field setting. But I also believe the greatest advances occur when theoretically-guided lab experiments are interpreted alongside results of field experiments that have less control, but greater reality. It is in that spirit that I now propose a set of complimentary field experiments that will attempt to generalize results from the lab.

Study 2. Mutual invasibility field experiments (years 2-3)
These experiments will take whole algal assemblages from eight natural ponds and reciprocally transplant them into mesocosms containing algal and herbivore assemblages from alternate ponds. The design is similar to the lab experiments, and to most common garden experiments that transplant species among assemblages. But these studies will quantify the ND and RFD of entire algal assemblages, and determine how ND/RFD influence the productivity of field assemblages.

<u>Study site</u>. The field experiments will be performed at the University of Michigan's Edwin S. George Reserve (Fig. 4A), which is a 525-hectare fenced research reserve located in Livingston County, Michigan ca. 25 miles Northwest of Ann Arbor (see accompanying letter of support from C. Dick, Director of the ESGR). My students and I have done survey and experimental work in several of these shallow ponds as part of my prior DIMENSIONS of Biodiversity grant. We have found that during July and August when our work is generally performed, phytoplankton tend to be dominated by chlorophyceans, desmidiales, and chlorococcales

Fig 4. Preliminary results from the E.S. George Reserve (ESGR). (A) Map of ESGR showing 45+ ponds and wetlands (red). Arrows give locations of Cattail and Experimental Ponds where my student and I have performed reciprocal transplant experiments. (B) Incidence matrix showing the presence (black) or absence (white) of 28 species in the two ponds and their phylogenetic relatedness. (C) Student performing transplant of algae from Cattail Pond into mesocosms with algae from Experimental Pond[86].



(green algae), with lesser representation of Bacillariophyceae (diatoms) and cyanobacteria. We have also found a rather high turnover of phytoplankton species among ponds, with an average 63% of species in any two ponds being unique. The field experiments described next will quantify mutual invasibility of all phytoplankton species in the ponds (not just green algae); however, by pre-sampling ponds just prior to set-up, I will try to choose ponds that maximize representation by green algae to make results as comparable as possible to the lab experiments.

My lab has performed reciprocal transplant studies of phytoplankton assemblages in select ponds at the ESGR to assess how the phylogenetic relatedness of species influences their ability to invade other assemblages. Fig. 4B shows an example of Cattail Pond and Experimental Pond, which had a total of 28 species of algae, with only two in common. After generating a molecular phylogeny, we performed a reciprocal transplant of species into mesocosms incubated *in situ* (Fig. 4C, and see Fig. F4 in *Facilities, Equipment, and Other Resources*). We found that species that invaded the alternate assemblage were no more, and no less differentiated phylogenetically than species that were unsuccessful[86]. Though performed for a different purpose, this study serves to demonstrate the feasibility of the transplant experiments.

Experimental design. With eight focal ponds, there are 28 possible reciprocal transplants of phytoplankton assemblages. I plan to complete half of these transplant experiments in year 2 of the grant, and half in year 3. Fig 5 gives an example of the design of one reciprocal transplant of assemblages from two hypothetical ponds (1, 2), each having two algal (a,b, vs. c, d) and one herbivore species (clipart). Experimental units for this study will be very high-tech … 2-L plastic soda bottles ☺. Though simplistic and inexpensive, they transmit light and hold H_2O temperatures well when incubated *in situ* (Fig. 4C). Not only do they mimic select physical conditions of resident ponds, they are sufficiently large to hold population sizes of $10^5 – 10^9$ algae cells that can grow for 20+ generations.

For each reciprocal transplant, I will establish six treatments in each of the two ponds involved (Fig. 5). Each treatment will be replicated 5× for 30 experimental units pond^{-1} (60 transplant^{-1}).

- *Treatments 1* and *2* will serve as controls to assess whether species that are transplanted from Pond 1 (2) can grow in the water of Pond 2 (1) in the absence of any competition with, or consumption by, the resident plankton. These treatments will ensure that any reduced growth rates that might be caused by an inhospitable environment will not be mistaken as evidence of species interactions. Growth rates of algal assemblages in *Treatments 1* and *2* will also be used as the baseline from which 'sensitivity' to competition and its modification by consumption will be calculated in subsequent treatments.

- *Treatments 3* and *4* will quantify how ND and RFD influence coexistence and biomass production of phytoplankton in the absence of consumption by macro-grazers. Phytoplankton will be transplanted from Pond 1 (2) into experimental units containing assemblages from Pond 2 (1) that have been grown to steady-state. The subsequent growth rate of each 'invading' species *i* from Pond 1 (2) will be used to calculate the sensitivity of the species to competition with resident algae in the absence of herbivory, $S_{i.-H} = (\mu_{i,Trmt1\ (2)} - \mu_{i,Trmt3\ (4)})/\mu_{i,Trmt1\ (2)}$.

- *Treatments 5* and *6* will quantify how ND and RFD influence coexistence and biomass production of phytoplankton in the presence of consumption by resident macro-grazers (those >250-μm). Phytoplankton will be transplanted from Pond 1 (2) into experimental units containing steady-state assemblages of algae and macro-grazers from Pond 2 (1). The subsequent growth rate of each 'invading' species *i* from Pond 1 (2) will be used to calculate the altered growth of each species caused by competition and herbivory, $S_{i.+H} = (\mu_{i,Trmt1\ (2)} - \mu_{i,Trmt5\ (6)})/\mu_{i,Trmt1\ (2)}$. The difference in sensitivities between Treatments 5 (6) verses Treatments 3 (4) indicate the change in competitive impacts due to macrograzers, $\Delta S_i = S_{i.+H} - S_{i.-H}$. Species with positive values of ΔS_i benefit from the presence of herbivores, whereas species with negative values are hurt by the presence of herbivores.

Experimental procedure. To begin an experiment, each of the experimental units assigned to a pond will be filled with 1.5-L of 0.2-μm filtered water from the resident pond, which we be exchanged at 10% per day. Bottles will then be randomly assigned to treatments 1-6, after which, treatments 3-6 will be inoculated with 10,000 cells mL^{-1} of phytoplankton from the appropriate assemblage (Fig. 5). For this study, phytoplankton will be collected from the 1 to 250-μm size fraction of filtered water samples, which will then be re-constituted in 0-2-μm filtered water prior to inoculation. My prior sampling and analyses suggest that nearly all primary producers fall within this size fraction.

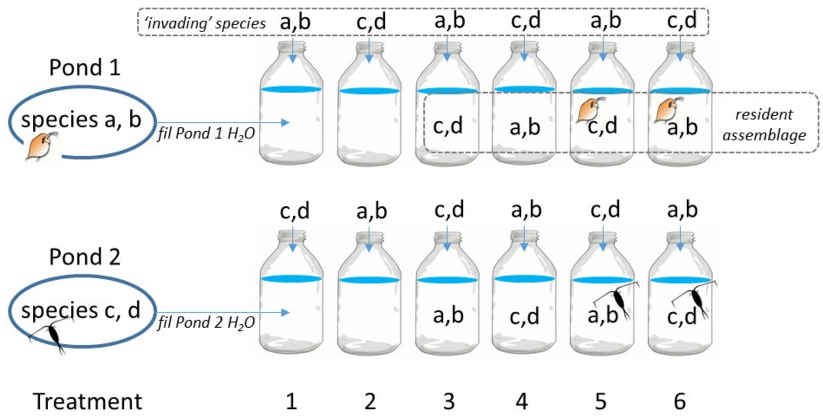


Fig 5. Experimental design of mutual invasibility field experiments. The figure depicts one example of a reciprocal transplant of algae among two ponds (1, 2) that each contain two species of algae (a,b vs. c,d) and one herbivore (clipart). Bottles represent six treatments per pond, with resident and invading assemblages noted.

After establishing resident phytoplankton assemblages, the experiment will proceed similar to the lab-based experiments. Rather than repeating details of the methods, I summarize them here noting any changes that are specific to the field experiment.

Algal growth curves. I will take three 5-mL subsamples from each experimental unit on each day of the experiment, analyze them for in-vivo fluorescence of the resident assemblage, and fit values to logistic growth curves $dF_i/dt = \mu_{i,res}F_i(1 - F_i/Fmax_i)$. These curves will be updated daily and used to ensure that mutual invasibility and measurements are taken at comparable points in the growth trajectory of the different experimental units. After measuring fluorescence, sub-samples will combined and preserved in 3% formalin. These will later be used to estimate population sizes of all species in the resident assemblage by counting cell densities on a hemacytometer, which will be fit to exponential growth curves $dN_i/dt = \mu_{i,res}N_i$ to quantify the per capita population growth rates, $\mu_{i,res}$, in the resident assemblage.

Mutual invasion. Once the resident assemblage reaches steady-state, species from the 'invading' phytoplankton assemblage will be introduced into experimental units at low density (10,000 cells mL^{-1}). At this time, I will also introduce macro-grazers into appropriate experimental units at densities equal to those in their originating ponds (determined from plankton tows taken prior to the start). Unfortunately, I cannot separate macro-grazers like cladocerns and copepods (> 250μm) from micro-grazers like ciliates and rotifers that overlap in size with phytoplankton (1-250μm). I will, however, count all types of grazers at introduction and throughout the study so that organisms not manipulated can be accounted for as covariates in the analyses should they reach notable densities.

After introduction of algal 'invaders' and herbivores, I will continue to take water samples every day to monitor fluorescence and cell densities of algal species until fluorescence values reach a new steady-state. At that point, I will take final measurements:

- *ND and RFD.* Cell densities of all invading phytoplankton species will be fit to exponential growth curves $dN_i/dt = \mu_{i,inv}N_i$ to estimate per capita population growth rates, $\mu_{i,inv}$. The subsequent growth rate of each 'invading' species *i* will be used to calculate their sensitivity to competition with resident algae in the absence of herbivores as $S_{i.-H} = (\mu_{i,Trmt1\ (2)} - \mu_{i,Trmt3\ (4)})/\mu_{i,Trmt1\ (2)}$, and in the presence of herbivores as $S_{i.+H} = (\mu_{i,Trmt1\ (2)} - \mu_{i,Trmt5\ (6)})/\mu_{i,Trmt1\ (2)}$. The difference, $\Delta S_i = S_{i.+H} - S_{i.-H}$, indicates whether phytoplankton species benefit from the presence of herbivores ($\Delta S_i > 0$), or are hurt by the presence of herbivores ($\Delta S_i < 0$). Sensitivities to competition will be used to calculate ND and RFD.

- *Biomass yields*. Steady-state biomass yield of each species, B_i, will be estimated by multiplying final population densities (cells mL^{-1}) by species-specific cell biovolumes (μm^3 $cell^{-1}$) and converting them to biomass (μg L^{-1}) assuming a specific gravity of 1.0. Total biomass of the assemblage is then $B_T = \sum B_i$'s.

- *Primary production*. Rates of net *(NP*) and gross photosynthesis (*GP*) will be measured by taking 500-mL subsamples from each unit, sealing them in airtight bottles, and measuring changes in dissolved [O_2] during light/dark incubations[70]. To ensure bottles measured on different dates are exposed to comparable light, I will perform incubations in a pondside incubation chamber. This chamber will have recirculating pond water to maintain ambient temperature, and will be fitted with a lid that has 12, 32-W GE cool-white 48" fluorescent lights powered by a portable generator. Though not comparable to ambient sunlight, I have used this method to saturate photosynthesis and measure production in a way that is standardized among treatments[71,72].

During all inoculation and sampling efforts, great care will be taken to ensure that species are not accidentally introduced into the ponds themselves. The experimental units themselves will remain fully sealed and water tight while they are incubated in the ponds. Units will also be removed and processed >15-m away from ponds during sampling, after which, they will be resealed and sterilized with 90% EtOH each time being returned to the ponds for incubation.

Statistical analyses and critical tests. The field experiments will allow me to quantify how the ND and RFD of entire algal assemblages influence the invasibility and productivity of natural ponds. Data analyses will be similar to those of the lab experiments, with two exceptions. First, ND and RFD will be quantified as the geometric mean and variance of all species sensitivities to competition [$ND = 1 - \prod_{i=1}^{n} S_i^{1/n}$, $RFD = \exp(\sqrt{\sum_{i=1}^{n}(\ln(S_i/ND)^2)/n})$]. It may be difficult for some to envision an mean ND or RFD among assemblages (as opposed to the ND or RFD among species-pairs in the lab experiments), but think about it like this … assemblages separated by larger ND's are composed of species that are, on average, less similar in resource requirements or grazer impacts than assemblages with smaller ND's. Second, because some species may invade successfully whereas others may not, there is no binary test of mutual invasibility or coexistence as in the lab experiment. Instead, I will test H1 by looking at how the difference ND – RFD influences the proportion of species that invade an assemblage. The proportion of species *p* that successfully invade from Pond 1 (2) into Pond 2 (1) will be logit transformed data to account for the bounded nature of proportions and modeled as, $y^* = \log(\frac{p}{1-p}) = \beta_0 - \beta_1(ND - RFD)$. As ND - RFD grows larger, H1 predicts that S_i's will, on average, grow smaller leading to a greater proportion of species that can successfully invade the alternative assemblage. Thus, if $\beta_1 > 0$ this will be interpreted as support for H1. To test H2, I will use a general linear model, $y = \beta_0 + \beta_1(ND - RFD) + \varepsilon$, where *y* is the log-transformed B_T, *NP*, *GP*, or *BSP*. If H2 is supported, I predict β_1 will be positive.

Limitations and future work. There are obvious limitations of the field experiments. First, the methods used in these experiments can only be used to estimate the mean ND among two communities, not the ND among species within the same community. In addition, because some species will be shared by different ponds, the ND and RFD calculated here are actually the ND and RFD among the unique species and the resident species (including shared species). Furthermore, it will be difficult to determine the underlying cause of ND and RFD in this experiment. Unlike the lab experiments where I will quantify species-specific biological traits and relate these to the ND and RFD among species pairs, I will not have that luxury for field assemblages. This represents the inherent trade-off empiricists face between experimental control vs. realism. And I view these field experiments as an important first step towards linking modern coexistence theory to the mutual invasibility and functioning of species assemblages.

Lastly, I can only manipulate size fractions of the plankton, rather than each individual species *per se*. This certainly leaves the door open for confounding by organisms that I cannot control (e.g., disease, micro-grazers, etc.). Still, this is the best I can do for a field test involving plankton. And by coupling the mechanistic, yet less realistic lab experiments with the more realistic, yet less controlled field experiments, I have put together what I believe is a strong test of H1 and H2 that spans from mechanistic process to real-world pattern.

INTELLECTUAL MERIT AND BROADER IMPACTS

Intellectual merit

The primary intellectual merit of this work will be to forge a better link between the causes and consequences of species coexistence. Many fields of ecology (e.g., *ecological stoichiometry*, *ecosystem engineering*, *biodiversity and ecosystem functioning*) have bridged ideas from community and ecosystem ecology by looking at how species interactions and the mechanisms that drive coexistence influence the ecological functions performed by individual species or groups of species. But work in these fields have rarely used modern theories of coexistence to determine how the balance of opposing forces (ND and RFD) influence coexistence and the functions performed by species. The work proposed here is an important first step towards understanding how mechanisms that control the outcome of species interactions simultaneously influence species coexistence and the ecological functions performed by species when together in an assemblage.

Broader impacts

In addition to disseminating results of the studies broadly to the scientific community via peer-reviewed publication and presentations, I have a number of broader impact activities planned, several of which represent programs I established with prior NSF support. Not only do these programs have demonstrated histories of success, I have worked to ensure they are executed properly by giving them a serious financial commitment in the budget ($21K) and by including letters of collaboration from the key people needed to make activities happen.

K-12 education

Leslie Science & Nature Center (http://www.lesliesnc.org/). With Broader Impacts funding from my last two NSF grants, I established a partnership with a local nonprofit organization that provides environmental education to >25,000 K-12 students annually. Working with staff of LSNC, my students, postdocs and I organize and lead two *'Aquatic Scientist'* summer camps per year (ca. 120 3rd to 6th graders). With waders, sampling nets, viewing boxes, and field microscopes in tow, we take kids on an exploration of ponds in the Black Pond Woods nature area to collect algae, invertebrates, and sometimes the unintended frogs and garter snakes that are too slow to escape curious minds. As kids collect, we teach them (i) how to use picture keys to identify the plants and animals, (ii) about the natural history of where species live and what they eat, and (iii) how to capture and release organisms responsibly. At the end of the exercise, each participant is given a sampling net and map of local ponds and encouraged to ask their parents to take them exploring. Many who attend these camps have never been outside the city, never explored an aquatic habitat, and are afraid to touch plants and animals. But by the end of the day, nearly 100% are wet, muddy, and excited to explore again ☺. I have requested $1K in years 1-3 for supplies needed to run two Citizen Science camps year^{-1} (see letter of support from S. Westhoff, Director LSNC).

Broadening participation in STEM

I have a strong history of enhancing participation by under-represented groups in STEM (see Results of prior NSF Support), and will continue that tradition with two activities tied to this grant:

High-school minority internships. Over the last 5-years I have partnered with the University of Michigan's Center for Engineering Diversity and Outreach (CEDO, http://cedo.engin.umich.edu/) to provide summer research internships for 12th grade students. Students are recruited from the Ypsilanti Public School District (64% African-American, 69% eligible for free/reduced lunch) and the Ann Arbor Rising Scholars program, which seeks to reduce achievement gaps between whites and under-represented students in the district. Interns work on independent research projects for 20 hrs wk^{-1} for 7 weeks, and receive a generous stipend and public transportation allowance. Students also receive 10-hours of tutoring per week in math, chemistry, physics, written/oral presentation, and preparation of college applications - all taught by UM work-study undergraduates. This experience not only exposes graduating seniors to research in aquatic sciences, it gives them the guidance needed to prepare for college and persist in achieving a university STEM degree. I have requested \$5K to support one intern $year^{-1}$ to work with my students and I on this project (see letter of support from L. Milton, Managing Director of CEDO).

Doris Duke Conservation Scholars Program. In 2016, U-M's School of Natural Resources and Environment received a grant from the Doris Duke Charitable Foundation to launch a new program to introduce greater diversity into the environmental conservation workforce. This program selects 20 undergraduates per summer through a nationwide competition, and immerses them as research assistants in PI labs for eight weeks. Internships are supplemented by a curriculum that incorporates minority history, culture, and experiences into students' learning of conservation practices. I will recruit two students $year^{-1}$ from this program to assist with summer research. The Doris Duke Foundation pays for room, board and a \$4,000 stipend; thus, I am requesting just \$1K $year^{-1}$ to supplement the program by sending my students to the Society of Freshwater Science's annual meeting to attend the 'Instars' workshop, which is a mentoring program for under-represented groups interested in freshwater ecology. A letter of support is provided from D. Taylor, Director of the Doris Duke Scholars Program.

Public education & outreach

Public lectures. As Director of the U-M / NOAA Cooperative Institute for Limnology and Ecosystems Research, I give 4-5 public lectures yr^{-1} to groups in Michigan (e.g., Sierra Club, Huron River Watershed Council) who invite me to talk about issues involving freshwater conservation (e.g., harmful algal blooms, invasive species, biodiversity loss). Although I do not request nor require any funding from NSF to continue these talks, I mention them as part of my broader impacts because I always acknowledge my funding from NSF, and emphasize the importance of support for research in ecological sustainability by NSF. I provide all attendees with brochures that have the contact information of state representatives, and ask that they call/write in support of science in the U.S.

RESULTS OF PRIOR NSF SUPPORT

DEB-1046121 DIMENSIONS: Can evolutionary history predict how changes in biodiversity impact the productivity of ecosystems? Amount: \$2,089,104. Period: 10/10 - 9/16. Intellectual Merit: This grant brought together ecologists, evolutionary biologists, and genomicists to determine how phylogenetic relatedness influences competition and coexistence of 50 widespread species of freshwater green algae. Broader Impacts: The grant supported 4 postdocs, 2 Ph.D. students, 3 M.S. students, and 16 undergraduates (inc. 9 women, 3 ethnic minorities, 5 now in STEM graduate programs). Products: 37 presentations at professional conferences, and 22 peer-reviewed papers[23,49,50,53,56,57,59,60,87-100], including four in *Nature* or *Science*, three in *Proceedings of the Royal Society B*, and three in *Ecology* or *Ecology Letters.* Several papers received significant media exposure, including a syndicated newspaper article by Reuters, and an NSF press conference.

EFRI-1332342 EFRI-PSBR: Biodiversity & Biofuels: Finding win-win scenarios for conservation and energy production. Amount: \$2,100,000. Period: 9/13 - 8/17. Intellectual Merit: This project represents a unique collaboration among ecologists, evolutionary biologists, and chemical engineers to test the hypothesis that naturally diverse groups of green algae have evolved to express complementary genes, metabolic pathways, and biological traits that enhance the efficiency and stability of algal biofuel production. Broader Impacts: The grant has supported 6 graduate students, 5 postdocs, and 27 undergraduates, and 3 technicians (inc. 24 women and 9 ethnic minorities). The project also established high-school and undergraduate internship programs for under-represented groups (9-12 minority students annually). Products to date: 14 presentations at professional conferences, 9 peer-reviewed publications[65,79,101-107] and 4 dissertations/theses[78,83,108,109].

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93 Cardinale, B. Overlooked local biodiversity loss. *Science* **344**, 1098, (2014).
94 Zimmerman, E. & Cardinale, B. J. Does biodiversity affect the productivity of natural lake ecosystems? *Oikos* **123**, 267-278, (2013).
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96 Cardinale, B. J. Towards a general theory of biodiversity for the Anthropocene. *Elementa* **1**, 000014 (2013).
97 Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. & O'Connor, M. I. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105-U129, (2012).
98 Cardinale, B. J. Biodiversity improves water quality through niche partitioning. *Nature* **472**, 86-89, (2011).
99 Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E. & Duffy, J. E. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods in Ecology and Evolution* **5**, 111-124, (2014).
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101 Hietala, D. C. & Savage, P. E. Reaction pathways and kinetics of cholesterol in high-temperature water. *Chemical Engineering Journal* **265**, 129-137, (2015).
102 Cardinale, B. J., Godwin, C. & Gregory, B. How frequently do algal polycultures out-produce their highest yielding species? . *Environ. Sci. Technol.*, (in review).
103 Narwani, A., A. Lashaway, D. Hietala, P. Savage & Cardinale, B. J. Effects of algal biodiversity on biocrude production and stability. *Environmental Science and Technology* **in review**.
104 Hietala, D. C., Koss, C., Narwani, A., B. J. Cardinale & Savage, P. E. Assessing biocrude quality from the hydrothermal liquefaction of microalgal polycultures. *Bioresour. Technol.*, (in review).
105 Byun, C. K., Carruthers, D., B. J. Cardinale & Lin, X. N. Transgressive over-yielding of algal bicultures in microdroplets. *Biotechnology and Bioengineering*, (in review).
106 M., A., Pankey, S., Narwani, A., Bentlage, B., Cardinale, B. J., Delwiche, C., Hietala, D. C. & Oakley, T. Algal polycultures enhance production and gene expression of lipids for biofuels. *Nature Communications*, (in review).
107 Faeth, J. L., Hietala, D. C. & Savage, P. E. A kinetic model for the fast and isothermal liquefaction of Nannochloropsis sp. *Algal Research*, (in review).
108 Hietala, D. *Developing a Comprehensive Model for the Hydrothermal Liquefaction of Microalgae* Ph.D. thesis, in progress thesis, University of Michigan, (2017 (expected)).
109 Carruthers, D. *An ecological and engineering approach to optimizing algal biofuels* M.S. thesis thesis, University of Michigan, Ann Arbor, (2016).

Biographical Sketch

Bradley J. Cardinale
Professor, School of Natural Resources and Environment
Professor, Department of Ecology and Evolutionary Biology
Director, Cooperative Institute for Limnology & Ecosystem Research (CILER)
University of Michigan, Ann Arbor, MI 48109
Email: bradcard@umich.edu
Phone: (734) 764-9689
Webpage: http://snre.umich.edu/cardinale/

(a) Professional Preparation

Arizona State University	Tempe, Az	B.S. in Biology	1993
Michigan State University	Lansing, MI	M.S. in Fisheries & Wildlife	1996
University of Maryland	College Park, MD	Ph.D. in Biology	2002
University of Wisconsin	Madison, WI	Postdoctoral fellow	2002-05

(b) Appointments

2016-	Director, NOAA-UM Cooperative Institute for Limnology & Ecosystem Research
2015-	Professor, School of Natural Resources and Environment, University of Michigan.
2015-	Professor, Dept. Ecology and Evolutionary Biology, University of Michigan.
2012-15	Associate Professor, School of Natural Resources and Environment, U-M.
2012-15	Associate Professor, Dept. Ecology and Evolutionary Biology, U-M.
2012-14	Director, Conservation Ecology Program, U-M.
2011-12	Assistant Professor, School of Natural Resources and Environment, U-M.
2011-12	Assistant Professor, Dept. Ecology and Evolutionary Biology, U-M.
2010-11	Associate Professor, Dept. Ecology, Evolution & Marine Biology, UC-Santa Barbara.
2005-10	Assistant Professor, Dept. Ecology, Evolution & Marine Biology, UC-Santa Barbara.

(c) Publications

Five publications most closely related to the proposed project. These have been selected from 96 peer-reviewed papers (cited 7516×, 18 papers with >100 citations, 12 highly cited papers ranking in top 1% for field of ecology).

1. [T]Fritschie, K. J., B. J. Cardinale, [P]M. A. Alexandrou, and T. H. Oakley. 2014. Evolutionary history and the strength of species interactions: testing the phylogenetic limiting similarity hypothesis. *Ecology*, 95:1407-1417.
2. Cardinale B. J., 2013. Towards a general theory of biodiversity for the Anthropocene. *Elementa,* 1: 000014 doi: 10.12952/journal.elementa.000014.
3. [P]Narwani, A., [P]M. A. Alexandrou, T. Oakley, [G]I. Carroll, and B. J. Cardinale. 2013. Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, 16:1373-1381.
4. Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, [P]P. Venail, [P]A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature, 486:59-67.
5. [G]Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology*, 92:1157-1165.

(Lab [P]postdoc, [G]graduate student, [U]undergraduate, [T]technician)

Five other significant papers

1. [G]Rakowski, C. and B. J. Cardinale. 2016. Herbivores control effects of algal species richness on community biomass and stability in a laboratory microcosm experiment. Oikos, doi:000. 1111/oik.03105.
2. Cardinale, B. J., K. Gross, [T]K. Fritschie, P. Flombaum, J. Fox, C. Rixen, J. van Ruijven, P. Reich, M. Scherer-Lorenzen, B. J. Wilsey. 2013. Biodiversity simultaneously enhances the productivity and stability of community biomass, but the effects are independent. Ecology 94:1697-1707.
3. Hooper, D. U., E. C. Adair, B. J. Cardinale, [P]J. E. K. Byrnes, B. A. Hungate, [U]K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. O’Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature, 486:105-108.
4. Cardinale, B.J. 2011. Biodiversity improves water quality via niche partitioning. Nature, 472:86-89.
5. Cardinale, B. J., [U]K. Matulich, D. U. Hooper, [P]J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O’Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany, 98: 572–592.

(Lab [P]postdoc, [G]graduate student, [U]undergraduate, [T]technician)

(d) Synergistic Activities

- Science Committee of *Future Earth*. I was nominated by the U.S. National Academy of Science to serve as a U.S. representative to the International Council of Science’s (ICSU) *Future Earth* initiative to unify the United Nation's Environmental Change Programs.

- Working groups. I have organized and led working groups at the National Center for Ecological Analysis and Synthesis (NCEAS, 2010-14) and the Socio-Environmental Synthesis Center (SESYNC, 2012-15). These efforts have brought together social and natural scientists, as well as engineers to summarize what is known about the role of biodiversity in the functioning of ecosystems, and to extend this knowledge to ecosystem services. These two working groups have produced a combined 37 data synthesis papers.

- Seminars & talks. I have given 73 invited seminars and talks (31 since 2010), and 81 submitted presentations. Recent examples include seminars at Univ. Chicago, Oxford Univ., Stanford Univ., and plenary addresses at the First International Congress on Biodiversity Conservation (Lima, Peru), and the Planet Under Pressure Conference (London, UK).

- Editorial boards. I have served as a member of the editorial board for *Ecology* and *Ecological Monographs* from 2009 to the present.

- Awards. In 2013 I was elected as a fellow to the American Association for the Advancement of Science (AAAS). In 2015 I was named by Thompson Reuters as one of *The World’s Most Influential Scientific Minds* – a distinction for researchers who have written the greatest number of papers designated by Essential Science Indicators as Highly Cited Papers from 2002-12 (ranking in the top 1% of citations for subject field of Environment/Ecology).

SUMMARY PROPOSAL BUDGET

YEAR 1

ORGANIZATION **University of Michigan Ann Arbor**				FOR NSF USE ONLY PROPOSAL NO.	DURATION (months) Proposed / Granted
PRINCIPAL INVESTIGATOR / PROJECT DIRECTOR **Bradley Cardinale**				AWARD NO.	

A. SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.7. show number in brackets)	NSF Funded Person-months CAL	ACAD	SUMR	Funds Requested By proposer	Funds granted by NSF (if different)
1. **Bradley J Cardinale - Professor**	0.00	0.00	0.50	6,758	
2.					
3.					
4.					
5.					
6. (0) OTHERS (LIST INDIVIDUALLY ON BUDGET JUSTIFICATION PAGE)	0.00	0.00	0.00	0	
7. (1) TOTAL SENIOR PERSONNEL (1 - 6)	0.00	0.00	0.50	6,758	
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. (1) POST DOCTORAL SCHOLARS	12.00	0.00	0.00	47,476	
2. (1) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	12.00	0.00	0.00	19,785	
3. (0) GRADUATE STUDENTS				0	
4. (3) UNDERGRADUATE STUDENTS				6,000	
5. (0) SECRETARIAL - CLERICAL (IF CHARGED DIRECTLY)				0	
6. (0) OTHER				0	
TOTAL SALARIES AND WAGES (A + B)				80,019	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				22,664	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A + B + C)				102,683	
D. EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $5,000.)					
TOTAL EQUIPMENT				0	
E. TRAVEL 1. DOMESTIC (INCL. U.S. POSSESSIONS)				2,000	
2. FOREIGN				0	
F. PARTICIPANT SUPPORT COSTS 1. STIPENDS $ 3,000 2. TRAVEL 1,000 3. SUBSISTENCE 400 4. OTHER 1,600					
TOTAL NUMBER OF PARTICIPANTS (0) TOTAL PARTICIPANT COSTS				6,000	
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				5,000	
2. PUBLICATION COSTS/DOCUMENTATION/DISSEMINATION				0	
3. CONSULTANT SERVICES				0	
4. COMPUTER SERVICES				0	
5. SUBAWARDS				0	
6. OTHER				1,000	
TOTAL OTHER DIRECT COSTS				6,000	
H. TOTAL DIRECT COSTS (A THROUGH G)				116,683	
I. INDIRECT COSTS (F&A)(SPECIFY RATE AND BASE) **MTDC (Rate: 55.0000, Base: 110683)**					
TOTAL INDIRECT COSTS (F&A)				60,876	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				177,559	
K. SMALL BUSINESS FEE				0	
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				177,559	

M. COST SHARING PROPOSED LEVEL $ 0	AGREED LEVEL IF DIFFERENT $		
PI/PD NAME **Bradley Cardinale**	FOR NSF USE ONLY INDIRECT COST RATE VERIFICATION		
ORG. REP. NAME* **Amy Holihan**	Date Checked	Date Of Rate Sheet	Initials - ORG

 ***ELECTRONIC SIGNATURES REQUIRED FOR REVISED BUDGET**

SUMMARY PROPOSAL BUDGET

YEAR 2

ORGANIZATION **University of Michigan Ann Arbor**				FOR NSF USE ONLY PROPOSAL NO.	DURATION (months) Proposed	Granted
PRINCIPAL INVESTIGATOR / PROJECT DIRECTOR **Bradley Cardinale**				AWARD NO.		

A. SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.7. show number in brackets)	NSF Funded Person-months CAL	ACAD	SUMR	Funds Requested By proposer	Funds granted by NSF (if different)
1. **Bradley J Cardinale - Professor**	0.00	0.00	0.50	6,960	
2.					
3.					
4.					
5.					
6. (0) OTHERS (LIST INDIVIDUALLY ON BUDGET JUSTIFICATION PAGE)	0.00	0.00	0.00	0	
7. (1) TOTAL SENIOR PERSONNEL (1 - 6)	0.00	0.00	0.50	6,960	
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. (1) POST DOCTORAL SCHOLARS	12.00	0.00	0.00	48,900	
2. (1) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	12.00	0.00	0.00	20,379	
3. (1) GRADUATE STUDENTS				29,606	
4. (3) UNDERGRADUATE STUDENTS				6,180	
5. (0) SECRETARIAL - CLERICAL (IF CHARGED DIRECTLY)				0	
6. (0) OTHER				0	
TOTAL SALARIES AND WAGES (A + B)				112,025	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				29,857	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A + B + C)				141,882	
D. EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $5,000.)					
TOTAL EQUIPMENT				0	
E. TRAVEL 1. DOMESTIC (INCL. U.S. POSSESSIONS)				5,000	
2. FOREIGN				0	
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $ 3,000					
2. TRAVEL 1,000					
3. SUBSISTENCE 400					
4. OTHER 1,600					
TOTAL NUMBER OF PARTICIPANTS (0) TOTAL PARTICIPANT COSTS				6,000	
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				10,000	
2. PUBLICATION COSTS/DOCUMENTATION/DISSEMINATION				3,000	
3. CONSULTANT SERVICES				0	
4. COMPUTER SERVICES				0	
5. SUBAWARDS				0	
6. OTHER				15,274	
TOTAL OTHER DIRECT COSTS				28,274	
H. TOTAL DIRECT COSTS (A THROUGH G)				181,156	
I. INDIRECT COSTS (F&A)(SPECIFY RATE AND BASE) **MTDC (Rate: 55.0000, Base: 163882)**					
TOTAL INDIRECT COSTS (F&A)				90,135	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				271,291	
K. SMALL BUSINESS FEE				0	
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				271,291	

M. COST SHARING PROPOSED LEVEL $ 0	AGREED LEVEL IF DIFFERENT $		
PI/PD NAME **Bradley Cardinale**	FOR NSF USE ONLY INDIRECT COST RATE VERIFICATION		
ORG. REP. NAME* **Amy Holihan**	Date Checked	Date Of Rate Sheet	Initials - ORG

 ***ELECTRONIC SIGNATURES REQUIRED FOR REVISED BUDGET**

SUMMARY PROPOSAL BUDGET

YEAR 3

ORGANIZATION **University of Michigan Ann Arbor**			FOR NSF USE ONLY PROPOSAL NO.	DURATION (months) Proposed	Granted
PRINCIPAL INVESTIGATOR / PROJECT DIRECTOR **Bradley Cardinale**			AWARD NO.		

A. SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.7. show number in brackets)	NSF Funded Person-months CAL	ACAD	SUMR	Funds Requested By proposer	Funds granted by NSF (if different)
1.	0.00	0.00	0.00		
2.					
3.					
4.					
5.					
6. (0) OTHERS (LIST INDIVIDUALLY ON BUDGET JUSTIFICATION PAGE)	0.00	0.00	0.00	0	
7. (1) TOTAL SENIOR PERSONNEL (1 - 6)	0.00	0.00	0.00	0	
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. (0) POST DOCTORAL SCHOLARS	0.00	0.00	0.00	0	
2. (1) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	12.00	0.00	0.00	20,990	
3. (1) GRADUATE STUDENTS				30,494	
4. (3) UNDERGRADUATE STUDENTS				6,365	
5. (0) SECRETARIAL - CLERICAL (IF CHARGED DIRECTLY)				0	
6. (0) OTHER				0	
TOTAL SALARIES AND WAGES (A + B)				57,849	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				13,492	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A + B + C)				71,341	
D. EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $5,000.)					
TOTAL EQUIPMENT				0	
E. TRAVEL 1. DOMESTIC (INCL. U.S. POSSESSIONS)				5,000	
2. FOREIGN				0	
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $ 3,000					
2. TRAVEL 1,000					
3. SUBSISTENCE 400					
4. OTHER 1,600					
TOTAL NUMBER OF PARTICIPANTS (0) TOTAL PARTICIPANT COSTS				6,000	
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				5,000	
2. PUBLICATION COSTS/DOCUMENTATION/DISSEMINATION				3,000	
3. CONSULTANT SERVICES				0	
4. COMPUTER SERVICES				0	
5. SUBAWARDS				0	
6. OTHER				15,838	
TOTAL OTHER DIRECT COSTS				23,838	
H. TOTAL DIRECT COSTS (A THROUGH G)				106,179	
I. INDIRECT COSTS (F&A)(SPECIFY RATE AND BASE) **MTDC (Rate: 55.0000, Base: 88342)**					
TOTAL INDIRECT COSTS (F&A)				48,588	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				154,767	
K. SMALL BUSINESS FEE				0	
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				154,767	
M. COST SHARING PROPOSED LEVEL $ 0	AGREED LEVEL IF DIFFERENT $				

PI/PD NAME **Bradley Cardinale**	FOR NSF USE ONLY INDIRECT COST RATE VERIFICATION		
ORG. REP. NAME* **Amy Holihan**	Date Checked	Date Of Rate Sheet	Initials - ORG

 ***ELECTRONIC SIGNATURES REQUIRED FOR REVISED BUDGET**

SUMMARY PROPOSAL BUDGET

Cumulative

ORGANIZATION: University of Michigan Ann Arbor				FOR NSF USE ONLY	
				PROPOSAL NO.	DURATION (months): Proposed / Granted
PRINCIPAL INVESTIGATOR / PROJECT DIRECTOR: Bradley Cardinale				AWARD NO.	

A. SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.7. show number in brackets)	NSF Funded Person-months CAL	ACAD	SUMR	Funds Requested By proposer	Funds granted by NSF (if different)
1. Bradley J Cardinale - Professor	0.00	0.00	1.00	13,718	
2.					
3.					
4.					
5.					
6. ( ) OTHERS (LIST INDIVIDUALLY ON BUDGET JUSTIFICATION PAGE)	0.00	0.00	0.00	0	
7. (1) TOTAL SENIOR PERSONNEL (1 - 6)	0.00	0.00	1.00	13,718	
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. (2) POST DOCTORAL SCHOLARS	24.00	0.00	0.00	96,376	
2. (3) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	36.00	0.00	0.00	61,154	
3. (2) GRADUATE STUDENTS				60,100	
4. (9) UNDERGRADUATE STUDENTS				18,545	
5. (0) SECRETARIAL - CLERICAL (IF CHARGED DIRECTLY)				0	
6. (0) OTHER				0	
TOTAL SALARIES AND WAGES (A + B)				249,893	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				66,013	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A + B + C)				315,906	
D. EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $5,000.)					
TOTAL EQUIPMENT				0	
E. TRAVEL 1. DOMESTIC (INCL. U.S. POSSESSIONS)				12,000	
2. FOREIGN				0	
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $ 9,000					
2. TRAVEL 3,000					
3. SUBSISTENCE 1,200					
4. OTHER 4,800					
TOTAL NUMBER OF PARTICIPANTS (0) TOTAL PARTICIPANT COSTS				18,000	
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				20,000	
2. PUBLICATION COSTS/DOCUMENTATION/DISSEMINATION				6,000	
3. CONSULTANT SERVICES				0	
4. COMPUTER SERVICES				0	
5. SUBAWARDS				0	
6. OTHER				32,112	
TOTAL OTHER DIRECT COSTS				58,112	
H. TOTAL DIRECT COSTS (A THROUGH G)				404,018	
I. INDIRECT COSTS (F&A)(SPECIFY RATE AND BASE)					
TOTAL INDIRECT COSTS (F&A)				199,599	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				603,617	
K. SMALL BUSINESS FEE				0	
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				603,617	
M. COST SHARING PROPOSED LEVEL $ 0	AGREED LEVEL IF DIFFERENT $				

PI/PD NAME: Bradley Cardinale	FOR NSF USE ONLY		
	INDIRECT COST RATE VERIFICATION		
ORG. REP. NAME*: Amy Holihan	Date Checked	Date Of Rate Sheet	Initials - ORG

C ***ELECTRONIC SIGNATURES REQUIRED FOR REVISED BUDGET**

Budget Justification

This budget is for a three-year period starting April 1, 2017 through March 31, 2020.

Salaries and Fringe Benefits

PI salary. Brad Cardinale (PI) is budgeted for 0.5 month of salary in the first two years of the project. This represents the effort level required for completing the proposed tasks. Salaries are based on a 9-month faculty appointments, with fringe benefits estimated at a rate of 30% of salary. The standard University of Michigan (UM) faculty benefits package includes health, dental, vision, and life insurance, and a retirement contribution. Additional information regarding UM faculty compensation and benefits may be found at: http://www.drda.umich.edu/proposals/budgets/staff_benefits.html.

Postdoctoral Fellow. The project includes funding for one Postdoctoral Fellow who will be paid in years 1 & 2 of the project to set-up, maintain, and sample the Mutual Invasibility lab experiments (years 1-2). Fringe benefits are estimated at a rate of 30% of salary. The standard University of Michigan benefits package includes health, dental, vision, and life insurance, and a retirement contribution.

Graduate student. The project includes funds for one Graduate Student Research Assistant (GSRA) who will lead the Common garden field experiments (years 2-3). GSRA support is budgeted at a 0.5 appointment level, and the stipend is based on the 2016-17 stipend rate (with an inflation rate of 1.03). GSRA benefits include the standard UM GSRA benefits package (Gradcare health, dental, and vision insurance). Additional information about GSRA health benefits may be retrieved at http://www.drda.umich.edu/proposals/students/gsra.html#health.

Technician support. The budget includes funds for a 50% technician (Tech 1) who will assist the postdoctoral fellow and graduate student on all aspects of the proposed experiments.

Undergraduate research assistants. The proposal supports 2 undergraduate assistants at $12 per hour each summer of the project. There are no benefits for summer hourly research assistants; the fringe rate is 7.65%. Assistants will help collect and process biological samples, including the counts of algae required to quantify yields through time.

Tuition

The budget includes graduate student tuition for the requested GSRA. This amount is UM's current established rate for graduate student tuition after advancement to candidacy. Tuition is estimated with 5% incremental increases for inflation in subsequent project years. Additional information regarding GSRA tuition rates may be found at: http://www.drda.umich.edu/proposals/students/gsra.html#tuition.

Travel (domestic and international)

Funds are requested for the PI, Postdoctoral Fellow, and/or Ph.D. student to make one trip per year to present their work at annual meetings or conferences. The travel budget has been developed based on airfare and lodging quotes available online and the University of Michigan's current mileage and per diem rates. Domestic travel has been estimated based on sample flight costs and daily expense rates for general domestic destinations. Additional funds are requested in years 2-3 to support vehicle rental from the U-M fleet for travel to/from the E.S. George field station for three summer months.

Facility users fee

We request $3,000 in years 2 & 3 to pay field-station expenses for use of U-M's E.S. George Reserve. Chris Dick, Director of the ESGR, has provided a letter of support.

Materials and Supplies
These costs include all technical items that are considered to be expendable, as well as, non-capital equipment items with a purchase price of less than $5,000 per item. Estimated expenditures, based on previous contracts, may include chemicals, solvents, glassware, and miscellaneous materials.

Publications
Publications charges are for fees, page charges, figure printing and/or off prints for peer review publications generated by the proposed project are budgeted at $3000 in years 2-3.

Broader impact activities (budgeted as 'Participant Support Costs', 'Support K-12 Education')

Leslie Science & Nature Center (*LSNC*). I request $1,000 in each of years 1-3 to support my planned K-12 education activities at the Leslie Science & Nature Center. Funds will pay for materials and supplies needed to run two Citizen Science camps per year for 120 3rd to 5th graders (sampling nets, plastic 5-gal aquaria, maps of local ponds). Costs are estimated based on previous summer camps my lab has organized. See accompanying letter of support from S. Westhoff, Director LSNC.

High-school minority internships. I request $5,000 in each of years 1-3 to partner with UM's Center for Engineering Diversity and Outreach to mentor one 12th grade student in a summer research internship. Students will be recruited from the Ypsilanti Public School District (64% African-American, 69% eligible for free/reduced lunch) and the Ann Arbor Rising Scholar program, which seeks to reduce achievement gaps between whites and under-represented students in the district. Interns will work 20 hrs wk^{-1} in the lab for 7 weeks, for which, they will receive a $3,000 stipends and a $400 allowance for public transportation. The remaining $1,600 will pay the work study fees for UM undergraduates who will tutor the high school interns for 10 hrs week^{-1} in math, chemistry, physics, written/oral presentation, and preparation of college applications. See accompanying letter of support from L. Milton, Managing Director of CEDO.

Doris Duke Conservation Scholars Program. The Doris Duke Conservation Program, which is designed to introduce greater diversity into the environmental conservation workforce, pays room and board and a $4,000 stipend to students who work with PI's in summer research. I request $1,000 per year to cap-off the program by sending my two summer students to the Society of Freshwater Science annual meeting to attend the 'Instars' workshop – a mentoring program for under-represented groups interested in freshwater ecology. See accompanying letter of support from D. Taylor, Director of the Doris Duke Scholars Program.

Total Direct Costs (TDC)
Total Direct Costs is the sum of all direct project costs and includes the categories of salaries, benefits, tuition, supplies and services, travel, and sub-contracts where applicable to the proposed program.

Modified Total Direct Costs (MTDC)
Modified Total Direct Costs is the cost basis used to calculate the indirect cost for a project. The MTDC is the TDC less the sum of tuition, equipment, participant costs, and sub-contracts where applicable to the proposed program. **Indirect Costs (IC)** The indirect cost rate of 55.5% is the standard rate established by the University of Michigan. **Total Sponsor Project Costs** Total cost is equivalent to the sum of TDC + IC where applicable to the proposed program.

Current and Pending Support

Investigator: Bradley Cardinale

Support: ☐ Current ☒ Pending ☐ Submission Planned in Near Future
Project/Proposal Title:
Linking species coexistence to the functioning of communities
(PI Bradley Cardinale)
Source of Support: NSF
Total Award Amount: $603,617 Total Award Period Covered: 04/01/17 – 03/31/20
Location of Project: Ann Arbor, MI
Person-Months Per Year Committed to the Project: Cal: Acad: Sumr: 0.5

Support: ☒ Current ☐ Pending ☐ Submission Planned in Near Future
Project/Proposal Title:
EFRI-PSBR: Biodiversity and biofuels: Finding win-win scenarios for conservation and energy production in the next century (PI Bradley Cardinale)
Source of Support: NSF
Total Award Amount: $1,999,612 Total Award Period Covered: 09/01/13 – 08/31/17
Location of Project:
Person-Months Per Year Committed to the Project Cal: Acad: Sumr: 1

Support: ☒ Current ☐ Pending ☐ Submission Planned in Near Future
Project/Proposal Title: Dimensions: Collaborative Research: Can evolutionary history predict how Changes in biodiversity impact the productivity of ecosystems (PI Bradley Cardinale)

Source of Support: NSF
Total Award Amount: $779,589 Total Award Period Covered: 10/01/10 – 09/30/16
Location of Project: Ann Arbor, MI
Person-Months Per Year Committed to the Project: Cal: Acad: Sumr:

Support: ☐ Current ☐ Pending ☐ Submission Planned in Near Future
Project/Proposal Title:

Source of Support:
Total Award Amount: Total Award Period Covered:
Location of Project:
Person-Months Per Year Committed to the Project: Cal: Acad: Sumr:

Support: ☐ Current ☐ Pending ☐ Submission Planned in Near Future
Project/Proposal Title:

Source of Support:
Total Award Amount: Total Award Period Covered:
Location of Project:
Person-Months Per Year Committed to the Project: Cal: Acad: Sumr:

FACILITIES, EQUIPMENT, AND OTHER RESOURCES

Primary lab. I maintain a 1200-ft^2 lab in the Dana Building on U-M's main campus, which is fully equipped for work with freshwater algae and invertebrates. The lab has a Percival AL-36 environmental chamber and laminar flow hood for algal culturing, a physically separated 'clean-lab' for nutrient analyses and water chemistry, a Fluid Imaging FlowCam with image recognition software for automated particle counting, a BioTek FLx800 microplate reader, two Olympus compound microscopes fitted with phase contrast and a digital imaging software for identification and analyses of algae. The lab also has four desktop computers with all software needed for this project.

Algal Culture Collection. My lab maintains a culture collection of 55 of the most abundant and widespread species of green algae identified in the U.S. EPA's 2007 survey of 1,200 lakes across North America (the National Lakes Assessment). For these species, we have generated an extensive database for measures of cell morphology and tissue stoichiometry (C, N, P). In addition, we have performed experiments in which we manipulated light intensities and nutrient (NO_3^-, PO_4^{3-}) concentrations in 1-mL well plates and quantified each species exponential growth rates when introduced at low cell densities. We then fit estimates of exponential growth rates to the Monod function, $\mu = \mu_{max}R/R(\mu_{max}/\alpha)$, where μ is the average growth rate at each light intensity or nutrient concentration R, μ_{Max} is the maximum growth rate a species achieves at unlimited intensity/concentrations, and α is the initial rate of change showing how growth rates respond at low intensity/concentrations. From the Monod function we estimated the minimum requirement (R^*) for light, N, and P where μ equals zero.

Table F1. Characteristics of 12 species to be used in the mutual invasibility lab experiments. Columns give the frequency of the genus in lakes throughout N. America, as well as the morphological (cell size and shape), physiological (light and nutrient affinities) and demographic (growth rates, carrying capacity) traits of the species. Data from Narwani et al.[49,53] and the 2007 EPA National Lakes Assessment.

Species	Frequency[1]	Cell size / shape[2]	Light affinity[3]	Nutrient affinity[4]	Cell stoichiometry[5]	Demographic param[6]
Ankistrodesmus falcatus	38, 12	302, 34, 2.09	0.06, 0.47, 14.87	14.87, 0.52, 0.00	55.90, 3.51, 0.33	0.37, 31755
Botryococcus sudeticus	17, 46	84, 14, 1.99	0.07, 0.76, 0.78	1.82, 0.55, 0.03	50.60, 3.59, 0.36	0.50, 23153
Chlorella sorokiniana	31, 21	75, 13, 1.94	0.05, 1.00, 1.04	1.16, 0.45, 0.05	49.70, 8.13, 0.87	0.95, 17861
Coelastrum microporum	24, 13	280, 10, 1.70	0.10, 0.91, 0.52	6.03, 0.49, 0.01	49.80, 5.33,0.59	0.40, 20729
Crucigenia tetrapedia	35, 17	160, 16, 2.09	0.04, 0.88, 1.23	2.84, 0.56, 0.02	56.90, 5.77, 0.73	0.26, 16879
Monoraphidium minutum	17, 48	113, 16, 1.20	0.07, 1.21, 0.79	3.59, 0.73, 0.01	52.30, 6.63, 0.68	0.31, 23871
Oocystis parva	71, 2	81, 19, 2.20	0.03, 0.72, 1.56	7.07, 0.51, 0.01	47.30, 5.86, 0.72	0.33, 25281
Oocystis polymorpha	71, 2	706, 14, 1.94	0.11, 1.38, 0.48	2.56, 0.74, 0.02	50.00, 4.63, 0.48	0.37, 19561
Pediastrum boryanum	20, 43	390, 11, 1.80	0.11, 0.65, 0.49	6.04, 0.50, 0.01	52.50, 5.15, 0.56	0.30, 16212
Pediastrum tetras	20, 43	1902, 12, 1.86	0.07, 0.86, 0.81	2.73, 0.38, 0.02	52.80, 5.84, 0.60	0.24, 21134
Scenedesmus acuminatus	53, 5	400, 20, 2.09	0.02, 1.08, 2.30	6.41, 0.69, 0.01	49.50, 5.20, 0.52	0.32, 26804
Selenastrum capricornutum	17, 38	159, 24, 2.42	0.10, 1.21, 0.51	3.88, 0.61, 0.01	52.10, 7.20, 1.07	0.45, 31897

[1]Frequency of occurrence of genus in N. American lakes (% lakes found, rank out of 262 genera)

[2]Species cell biovolumes (μm^3), elongation (larger values = more elongated), and roughness (larger values = non-convex perimeters).

[3]Growth response to increasing light (d-1/µmol L-1), max specific growth (d-1), and min light required for positive growth (µE/m2/sec).

[4]Growth response to increased NO3 (d-1/µmol L-1), max specific growth (d-1), and min required for positive growth (µmol/L).

[5]Percent carbon, nitrogen, and phosphorus in the dried algal biomass.

[6]Maximum per capita growth rates (μ_{max}, d-1), and carrying capacity (K, cells mL-1) when grown in COMBO culture media.

Select functional traits of the 12 taxa proposed for use in the laboratory experiments of the current proposal are shown Table F1. Figure F2 shows their sensitivity to competition, niche differences, and relative fitness differences.

Mesocosm facility. PI Cardinale maintains a 1,600-ft^2 facility on the main campus at U-M that houses 180, 9.5-L continuous flow chemostats. The lab was designed by Aquaneering Inc.

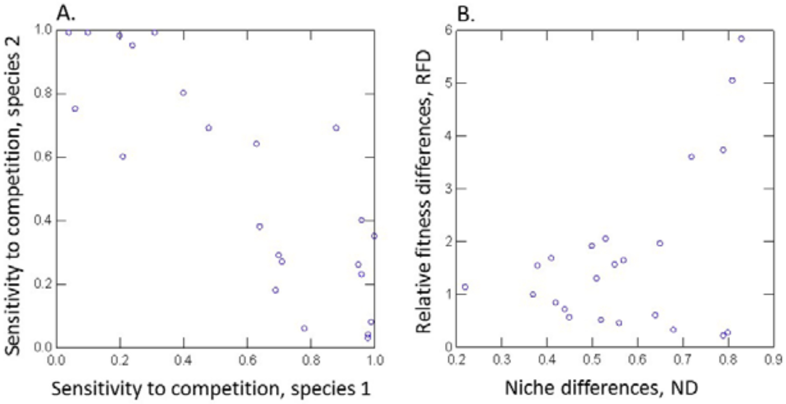

Fig F2. Results of a pilot study in which I grew 24 combinations of the 12 species in Table F1 in small (1-mL) well-plates and measured *mutual invisibility*. Panel A shows the species sensitivity to competition (each dot represents one species pair), while panel B shows their ND and RFD. This subset of 24 combinations exhibited the full range of competitive interactions , suggesting the species pool will capture the variation needed to describe how ND and RFD influence coexistence and ecological function

specifically for the purpose of culturing algae to steady-state biomass. There are six racks, ea. with 30 chemostats fed water from holding tanks below. Holding tanks have chillers that maintain H_2O temperature constant at ranges between 16 and 22 C°, and are themselves supplied by a 1,000-L media tank. Lighting below the chemostats consist of four T5 fluorescent lamps that emit full spectrum light at 250 μE m^{-2} sec^{-1} (sufficient to saturate algal growth).

Fig F3. Pictures of the experimental chemostat facility at the University of Michigan.

<u>*Edwin S. Georges Biological Reserve.*</u> The *field experiments* will be performed at the E.S. Georges Biological Reserve, which has been administered as a research station by U-Michigan since 1930. ESGR is a 525-hectare fenced preserve located in Livingston County, Michigan (about 25 km Northwest of Ann Arbor). A rich history of long- and short-term biological studies has been conducted on the ESGR. More than 475 research papers, 81 Ph.D. dissertations, and 31 Masters theses have been published from studies carried out in the ESGR, many of which stem from work done in the 45+ ponds and wetlands located on the reserve. The reserve has 180, 1,200-L cattle tanks available for use in our research (Fig. F4). The current director – Chris Dick - has provided a letter of support for our work.

Fig F4. Pictures of one reciprocal transplant study being performed at the E. S. George Reserve.

Data management plan

Types of data, physical samples and collections

The research I have proposed will produce two primary datasets – one associated with the Mutual Invasibility Lab Experiments, and one associated with the Mutual Invasibility Field Experiments. In addition, the laboratory experiments will produce voucher specimens of algae for purposes of verifying identifications.

Standards for data types

All data from the proposed experiments will be published with peer-reviewed papers as summarized datasets with accompanying metadata. Metadata standards vary among journals, and among disciplines. So in addition to publishing summarized datasets with papers, I will also make all raw data publicly available in the Knowledge Network for Biocomplexity (KNB). KNB is funded by NSF's Knowledge and Distributed Intelligence Program, and represents a collaboration between the National Center for Ecological Analysis and Synthesis (NCEAS), the Long Term Ecological Research Network (LTER), Texas Tech University, and the San Diego Supercomputing Facility. KNB uses a data management software package that has been extensively used by working groups at NCEAS to manage the large datasets generated in synthesis projects. Metadata is formatted according to standards of the Ecological Metadata Language (EML), which is a metadata specification developed by the ecology discipline and for the ecology discipline based on work and recommendations by the Ecological Society of America.

Roles and responsibilities of all parties

This is a sole PI grant, so Cardinale will ultimately be responsible for ensuring that all aspects of the Data Management Plan are adhered to. Cardinale will review this Data Management Plan with all postdoctoral fellows and students working on the project to make sure they understand their responsibilities for data management and sharing.

Dissemination of methods, and PI policies for data sharing and public access

Project datasets, which represent summarized data that accompany manuscripts, will always be made publicly available at the time of publication. The raw datasets and biological samples will be made available within 3-years of original collection. I believe this 3-year window is essential for ensuring that PI's can perform quality control and analysis of datasets, and have first publication rights. However, I will also consider requests from researcher for unpublished data or non-archived samples under the constraint that individuals request explicit written permission from data provider, and I can ensure that use of the data does not interfere with my own ongoing data summaries or publications.

I would note that I have a strong history of making data associated with my publications publicly available, and I have routinely published datasets from my synthesis efforts to make those data publicly available. I am a staunch advocate for data accessibility post-publications, especially for tax-payer funded projects.

Data archiving

Project datasets. In addition to publishing summarized datasets with papers, I will also make all raw data publicly available in the Knowledge Network for Biocomplexity (KNB). KNB is funded by NSF's Knowledge and Distributed Intelligence Program, and represents a collaboration between the National Center for Ecological Analysis and Synthesis (NCEAS), the Long Term Ecological Research Network (LTER), Texas Tech University, and the San Diego Supercomputing Facility. KNB uses a data management software package that has been extensively used by working groups at NCEAS to manage the large datasets generated in synthesis projects. Metadata is formatted according to standards of the Ecological Metadata Language (EML), which is a metadata specification developed by the ecology discipline and for the ecology discipline based on work and recommendations by the Ecological Society of America.

Biological samples. Taxa proposed for use in the laboratory studies (see Table F1, *Facilities, Equipment and Other Resources*) were obtained from the Culture Collection of Algae administered at the University of Texas Austin through the College of Natural Sciences. This collection has been around since 1952, has a curator, is funded by the National Science Foundation, and receives additional funds as a non-profit through sale of cultures. By publishing UTEX catalogue numbers for the species used in the experiments, I can ensure future researchers have access to a reliable source of the original strains. In addition, I plan to process and place permanent voucher slides, photos, and preserved mRNA samples of all algal species in the herbarium of the New York Botanical Garden.

Postdoctoral mentoring plan

History of mentoring. I have a strong history of postdoctoral mentoring. To date, I have advised twelve postdocs, two of whom are current:

Sarah Jackrel 2016-present
Casey Godwin 2015-present
Shovon Mandal 2014-15 (Postdoc, UC-San Diego)
Anita Narwani 2011-14 (Junior Group Leader, EAWAG Switzerland)
Daniel Allen 2012-14 (Assistant Professor, Arizona State University)
Konrad Kulacki 2009-13 (Biologist, Exponent Consulting, Boston MA)
Patrick Venail 2011-13 (Assistant Professor, University of Geneva)
Ryan Utz 2010-11 (Assistant Professor, Chatham University)
Jarrett Byrnes 2008-10 (Assistant Professor, University of Massachusetts)
Carolyn Kurle 2008-10 (Assistant Professor, University of California-San Diego)
Steven Zeug 2007-09 (Fisheries biologist, Cramer Fish Sciences, CA)
Marc Cadotte 2006-07 (Professor, University of Toronto)

These postdocs have led or co-authored 32 peer-reviewed publications, including numerous papers in *Nature*, *PNAS*, *Ecology*, and *Ecology Letters*. I have helped these scholars secure ca. $180K in funding, including an NSF Postdoctoral Fellowship (D. Allen) and the prestigious Karp Fellowship from the University of California (C. Kurle). Postdocs have landed top faculty positions at UC – San Diego (C. Kurle), U-Geneva (P. Venail), U-Massachusetts (J. Byrnes), U-Oklahoma (D. Allen), and U- Toronto (M. Cadotte).

This project will support on postdoctoral fellow who will be responsible for completing the field experiments. Like all of my postdocs, this individual will have the following mentoring program:

Orientation. Upon hire, I will meet with the postdoc to discuss and agree on mutual expectations: (a) the amount of independence and flexibility of the job, (b) expected interaction with coworkers, (c) expected levels of productivity, including scientific publications, (d) work habits and laboratory safety, and (e) the importance of data management and documentation of research methodologies.

Individual Development Plan (IDP). Following orientation, the postdoc will be expected to prepare an IDP within one month of his/her start date. The IDP will contain (a) a statement of career goals, (b) experience and products needed to achieve career goals, (c) an outline of how the postdoc will attain the appropriate experience and products, and (d) a timeline for success as a postdoctoral researcher. The IDP will be reviewed every 6-mo. to gauge the success of the postdoc in meeting his/her goals.

Research proposal. Within three months of hire, the postdoc will be required to submit a written research proposal that details a set of novel questions and hypotheses that complement the broader goals of this proposal, and which outlines the approaches and methodologies they will use to establish their own independent research projects. In addition to gaining experience with writing their postdoctoral research proposal, I routinely include my postdoctoral fellows in the preparation of my own grant proposals, as well as in reviewing grant proposals to provide further experience.

Career Counseling. Each fall, I lead a 2 day workshop at U-Michigan that trains postdocs in key aspects of academic jobs: (a) the interview process – practice of job talks, as well as preparation for common interview questions, (b) a mock NSF panel review where postdocs review donated proposals that have both succeeded and failed in getting funded, and (c) dealing with the media, which includes practice interviews.

The U-M's Center for Research on Learning and Teaching offers a similar 3-day program in Professional Development for Postdoctoral Scholars (PDPDS) that focuses on: (a) teaching and mentoring, (b) communicating science, and (c) networking and interviewing. The curriculum is comprised of proposal writing workshops, teaching and mentoring sessions, workshops in job search strategies, and mock grant review panels.

Teaching Skills. This position is not a teaching postdoc, and the individual that is hired will not be required to develop classes. However, I will mentor the postdoc to make sure they have the have the appropriate amount of experience needed to land their anticipated position.

One way I accomplish this is by routinely making opportunities available for postdocs to give guest lectures in my classes, and I sometimes develop graduate seminars with postdocs as co-instructors to help build their CV's. This allows me to speak explicitly to their teaching skills when I write a letter of recommendation.

In addition, the U-M's Center for Research on Learning and Teaching offers a 7-week short course for postdocs who wish to gain experience with course development, and get feedback on teaching styles. Through this course, postdocs learn about the latest research on memory, learning and teaching, become familiar with the use of instructional technology, develop a course syllabus, and get constructive feedback on their teaching styles.

To: NSF Division of Environmental Biology Program

From: Christopher Dick
Professor and Curator
Director, University of Michigan Herbarium
Director, ES George Reserve

By signing below, I acknowledge that I am listed as a contributor on this proposal, entitled *"Linking species coexistence to the functioning of ecosystems,"* with Bradley Cardinale as the Principal Investigator. I agree to accommodate your request to conduct research in the University of Michigan's E.S. George Reserve, as described in the project description of the proposal, and I commit to provide or make available the resources specified therein.

Signed:

Organization: University of Michigan

Date: July 20, 2016

MICHIGAN ENGINEERING

UNIVERSITY of MICHIGAN ■ COLLEGE of ENGINEERING

To: NSF Division of Environmental Biology Program

From: Lyonel J. Milton
Managing Director
Center for Engineering Diversity and Outreach (CEDO)
University of Michigan

By signing below, I acknowledge that I am listed as a contributor on this proposal, entitled *"Linking species coexistence to the functioning of ecosystems,"* with Bradley Cardinale as the Principal Investigator. The Center for Engineering Diversity and Outreach will partner with Dr. Cardinale to help recruit and mentor high school students for summer internships, as described in the project description of the proposal, and I commit to provide or make available the resources specified therein.

Signed:

Organization: University of Michigan

Date: July 23, 2016

UNIVERSITY OF MICHIGAN
SCHOOL OF NATURAL RESOURCES AND ENVIRONMENT

To: NSF Division of Environmental Biology Program

From: Dorceta E. Taylor, Professor
James E. Crowfoot Collegiate Chair
Director of Diversity, Equity, and Inclusion
Director Doris Duke Conservation Scholars Program

By signing below, I acknowledge that I am listed as a contributor on this proposal, *entitled "Linking species coexistence to the functioning of ecosystems,"* with Bradley Cardinale as the Principal Investigator. I agree to partner with the Professor Cardinale to help recruit and mentor undergraduate students through the Doris Duke Conservation Scholars Program, as described in the project description of the proposal, and I commit to provide or make available the resources specified therein.

Signed: Dorceta E. Taylor

Organization: University of Michigan

Date: July 22, 2016

Leslie
SCIENCE & NATURE
Center

To: NSF Division of Environmental Biology Program

From: Susan Westhoff
Executive Director
Leslie Science and Nature Center (LSNC)

By signing below, I acknowledge that I am listed as a contributor on this proposal, *entitled "Linking species coexistence to the functioning of ecosystems,"* with Bradley Cardinale as the Principal Investigator. I agree to partner with the Dr. Cardinale to develop and execute Aquatic Scientist camps at LSNC as part of his K-12 education plan, as described in the project description of the proposal, and I commit to provide or make available the resources specified therein.

Signed: Susan Westhoff

Organization: Leslie Science and Nature Center

Date: July 22, 2016