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REVSYS: Systematics of Amelanchier (Rosaceae)

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Accomplishments

* What are the major goals of the project?

The first goal of this proposal is a taxonomic revision of *Amelanchier.* These shrubs and small trees are native to every state in the United States except Hawaii, all Canadian provinces and territories, and sporadically in Eurasia. This genus is important ecologically in early succession, it is used for landscape plantings, and its fruits are eaten by wildlife and are a minor fruit crop. Shadbushes or serviceberries, as these plants are commonly called in North

America, are difficult taxonomically. Past species classifications of the genus have frustrated people who work with these plants, such as botanists, horticulturists, wildlife ecologists, conservation biologists, land-use managers, and others. The source of the difficulty is that *Amelanchier* polyploids are apomictic (seed production is asexual). Apomictic groups diversify differently from sexual groups and form different kinds of groups. Application of species concepts used in sexual groups to apomicts is problematic (see below). We have focused on understanding diversification in apomictic *Amelanchier*. We have studied diversification through extensive field work of all major taxa from much of the geographic range of the genus. We have collected data on morphology, ploidy (number of genomes), the occurrence of apomixis and hybridization, DNA sequences, GPS, and flowering time. We aim to construct a species classification of the genus founded on our understanding of diversification. We also want our classification it to be usable by people who work with the genus and to include as much diversity in the genus as possible.

The second goal is training of undergraduate and graduate students in plant systematics and revisions (monographs). The skills in this training include fieldwork, quantitative morphology, flow cytometric determination of ploidy level and reproductive mode (sexuality and apomixis), molecular phylogeny, and nomenclature. These skills are essential to understanding and communicating about plant species generally and highly complex apomictic groups like *Amelanchier* specifically. Michael Burgess completed a Ph.D. on *Amelanchier* in 2010 and is now in a tenure-track position at The State University of New York, Plattsburg. We continue to collaborate with him on *Amelanchier.* Current Ph.D. student Eric Doucette and current M.S. student Kevin Cushman are playing central roles in this research, and several undergraduates have participated, including two who completed senior theses on *Amelanchier*.

* What was accomplished under these goals (you must provide information for at least one of the 4 categories below)?

Major Activities:

<u>Fieldwork</u> – We continue our commitment to field studies to help us understand diversification, ecogeographic variation, and hybridization in *Amelanchier* and to obtain material to study morphological variation, document ploidy level and apomixis, and carry out DNA sequencing for phylogenetic analyses. These diverse data provide the basis for understanding diversification in *Amelanchier* and determination of species status and relationships.

Our primary needs in 2013 were to increase sampling of diploids in *Amelanchier bartramiana* in northeastern North America, *A. ovalis* on Crete and in Spain, and *A. pallida* in northern California and southern Oregon. We also wanted to carry out fieldwork in the Canadian Maritime provinces, wherein fieldwork prior to this grant showed considerable variation in *Amelanchier.* Other than one field trip to Nova Scotia in 2011, we had not sampled this region sufficiently.

In 2013 graduate students Kevin Cushman and Eric Doucette and I drove about 17,300 miles to make 291 plant collections in seven states (Arkansas, California, Kentucky, Maine, New Hampshire, Oregon, and Vermont), five Canadian provinces (British Columbia, New Brunswick, Nova Scotia, Prince Edward Island, and Quebec), Greece, and Spain. Below is a list of individual trips.

1. ME, NH, and VT – Doucette; 4-11 May (not continuous) 2013; 15 individuals of *Amelanchier*
2. ME, New Brunswick, Nova Scotia, Prince Edward Island, and Quebec – Cushman; 6-31 May (not continuous) 2013; 186 individuals of *Amelanchier*
3. CA, OR – Doucette; 15-22 May 2013; 48 individuals of *Amelanchier*

4. Greece (Crete) – Campbell; 13 May 2013; one individual of *Amelanchier*
5. Spain – Campbell; 19-21 May 2013; 21 individuals of *Amelanchier*
6. ME, NH, and VT – Doucette; 15 June 2013; recollecting *Amelanchier* from trip 1
7. CA, OR – Doucette; 30 June – 4 July 2013; recollecting *Amelanchier* from trip 3
8. ME, New Brunswick, Nova Scotia, Prince Edward Island, and Quebec – Cushman; 7-17 July 2013; recollecting *Amelanchier* from trip 2
9. AR, KY – Doucette; 1-2 August 2013, six individuals of *Amelanchier*
10. British Columbia – Campbell; 28 August 2013; 11 individuals of *Amelanchier*

In 2013, we also obtained 10 specimens from colleagues from five states (Florida, Indiana, Ohio, Missouri, and Pennsylvania) and Germany. This year's effort brings to a total for this project of over 1500 collections from 42 US states (all except HI, IA, KS, LA, MS, NE, OK, and TX), eight Canadian provinces, and 11 Eurasian countries (Austria, China, France, Germany, Greece, Japan, Korea, Moldava, Montenegro, Russia, and Spain). We tried to get material from Louisiana and Mississippi in 2013, but could not find *Amelanchier* in areas where it had been previously collected.

Before this project began, we knew that we needed to create a solid morphological sample of the genus because 95% or more of herbarium specimens have only flowering, fruiting, or vegetative material. We have collected specimens with flowering and fruiting material from the same individual for almost all of our accessions, which requires separate field trips several weeks apart. Importantly, such complete collections permit larger morphological datasets with data from flowering and mature foliage and fruit. For all our collections, we recorded GPS coordinates that we are using in geographical analyses. For some collections we collected seeds for flow cytometric determination of reproductive mode. For many of our collections, we took pictures for the *Amelanchier* website (http://biology.umaine.edu/Amelanchier/). In 2013 we continued making exsiccatae, multiple collections from the same individual. This year we made exsiccatae for six individuals and now have exsiccatae for almost all the major taxa we will include in our classification. Our exsiccatae comprise a reference collection for the major taxa of our classification that will be distributed to major herbaria in the northern hemisphere (where *Amelanchier* is native). We will send a set of most of our collections to one or two major U.S. herbaria and sets of accessions from particular regions of the U.S. and Canada to important regional herbaria of the region.

Morphology – Since February 2013, we have scored about 150 complete collections for 47 morphological characters (variables), bringing the total number of individuals scored to over 1000. For 33 of these characters, we perform replicate scoring of at least five structures. For example, on each specimen, we measure the length of five petals and the number of styles in five flowers. The characters include many that have been traditionally used in the taxonomy of the genus, allowing us to evaluate their utility. We are also scoring new characters to test their usefulness. We analyze these morphological data with basic statistics, principal components analysis, clustering, and other approaches using the software R. We are using these analyses -- along with information about ploidy level, ecogeography, DNA sequence data, and flowering time -- to clarify the species problem and construct a new species classification in *Amelanchier*.

Determination of ploidy level and reproductive mode – Flow cytometry (FC) is a powerful tool because it is rapid, and it identifies the major shift from diploidy to polyploidy. In *Amelanchier* this shift is usually associated with a transition from sexuality to apomixis and from cohesive diploid taxa to taxonomically complex polyploids. Therefore, we have made a large commitment to FC determination of ploidy. We assayed ploidy level in almost all the plants we collect on our 2013 field trips. We now have ploidy level determinations for over 1,350 plants, including all major taxa in the world. We are also using flow cytometry to document apomixis.

Molecular phylogeny – We continue to use three nuclear regions: the internal transcribed spacer of nuclear ribosomal DNA (ITS), the external transcribed spacer of nrDNA (ETS), and the second intron of the LEAFY gene. The LEAFY gene is single copy in many plant groups, and data from apple show that it was duplicated, presumably in the allopolyploid origin of the tribe Pyreae (the group to which *Amelanchier* belongs). We recover two strongly divergent sets of sequences that are homologous to *AFL*1 and *AFL*2 in apple and that we assume represent paralogs that arose during the origin of the Pyreae. Most of our data come from *AFL*2. Over the course of this grant we have obtained almost 1300 sequences (mostly cloned) of *AFL*2, ETS, and ITS, 400 from 65 diploid individuals and 900 from 100 polyploids. We have also obtained sequences from four chloroplast regions (rpoB-trnC, trnD-trnT, trnHb-rpl2, ycf6-psbM) for 51 diploid and 38 polyploid individuals.

We continue to use molecular data for insights into the taxonomic status of diploids and their relationships to one another. We also continue to explore the origins of polyploids based on their AFL2 sequences set on our diploid, nuclear and chloroplast phylogenies.

Specific Objectives: The objectives are to

1. assemble data about morphology, DNA sequences, ploidy level, reproductive mode, reproductive isolation, and geographic distribution in Amelanchier;

2. use these data to delimit species and monograph the genus, with formal descriptions, full nomenclatural treatment, keys, geographic distributions, and discussion;

3. make this revision available to scientists and the public through publications and our website (http://biology.umaine.edu/Amelanchier/), with online keys linked to supporting images and taxonomically useful information;

4. train graduate and undergraduate students in revisionary systematics;

5. attract underrepresented students to this research by giving them solid experiences in the lab, field, and other opportunities to learn about plants; and

6. provide outreach by presenting two workshops to give K-12 teachers exercises in pollination biology for their students.

Significant Results:

Determination of ploidy level and reproductive mode – For 285 samples collected in 2013 for which we determined ploidy, 89 are diploid, 11 triploid, and 185 tetraploid. The proportion of the three ploidy levels – 31% diploid, 4% triploid, and 65% tetraploid – are close to the those in the totals sample of over 1350 individuals. We added significant diploid collections for *A. bartramiana* in Maine, New Brunswick, Nova Scotia, Prince Edward Island, and Quebec; *A. ovalis* in Spain, and *A. pallida* in California and Oregon. In 2013, we documented diploidy in *A. semiintegrigolia,* which had formerly been known only as a polyploid. Our one collection of *A. ovalis* from Crete, which has been classified as subsp. *cretica*, is tetraploid. We were fortunate that this taxon was in full flower when we collected it and that it was growing on cliff faces inaccessible to goats, which have apparently eliminated it from accessible, surrounding areas. We collected this subspecies on mainland Greece in 2010, also as tetraploid, but from only two nearby individuals that were not yet in flower. These new accessions, plus numerous others from this year, will help us understand these taxa more thoroughly.

Diploids are critical to understanding *Amelanchier* diversification because they contribute genomes to the polyploids and thus provide a context for understanding polyploids. So far, we have documented diploidy in 12-13 species, including five restricted to eastern North America, three restricted to western North America, one that ranges from Vermont to Montana and Québec to Manitoba (and, based on morphology and not ploidy, southern Sakatechewan). There are diploids in two species from Europe (ploidy has not been determined for these two taxa where they grow in western Asia and North Africa) and in one or two closely related species from eastern Asia. All the diploids, with the possible exception of eastern Asian *A. asiatica* and *A. sinica*, are morphologically, ecogeographically, and mostly genetically distinct.

Morphology – All diploid *Amelanchier*, with the possible exception of *A. asiatica* and *A. sinica*, are morphologically distinct from one another. Each diploid has several diagnostic morphological character states, although there often are, as noted below, morphological differences (often slight) between diploids and polyploids.

Morphology gives us some clues about the ancestry of polyploids. For example, before we had *AFL*2 DNA sequences, we predicted that, if *A. spicata* (often called *A. stolonifera*) is an allopolyploid, one of its parents was *A. humilis* because of the shared rhizomatous habit, short petals, erect and densely flowered racemes, and leaves that are hairy at flowering and similar in shape. We thought the other parent of an allopolyploid *A. spicata* could be *A. canadensis. AFL*2 confirmed that *A. humilis* and *A. canadensis* contributed genomes to *A. spicata,* which also includes a genome from *A. bartramiana*.

Molecular phylogeny – We are using molecular data to determine the taxonomic status of diploids and their relationships to one another. The occurrence of allelic monophyly in a diploid taxon is good evidence that it is a distinct evolutionary lineage. Diploids form three major clades. Clade A consists of western North

American taxa plus *A. humilis* from eastern North America, clade B contains remaining eastern North American taxa, and clade O encompasses Old World taxa. Our molecular data and morphological synapomorphies strongly support clades A and B. Clade O is moderately supported, as is its sister-group relationship to clade B.

In our sample of about 100 polyploids, most are allopolyploids with two or three diploid ancestors. In some individuals, multiple *AFL*2 clones all nest strongly with a diploid and are potentially autopolyploid, but ETS reveals two diploid ancestors and therefore allopolyploidy. In other individuals whose multiple *AFL*2 clones all nest strongly with a diploid, we have not yet further tested autopolyploidy.

Progress toward a species classification of *Amelanchier* – We have resolved three challenges that stem from the way *Amelanchier* polyploidy apomicts diversify. For all nine North American diploids and European *A. ovalis*, we have documented morphologically quite similar polyploids*.* We call this **semi-cryptic ploidy variation**. We postulate that polyploids resemble a diploid due to genetic segregation favoring one of the diploid ancestors in allopolyploids, backcrossing of allopolyploids with one diploid ancestor, or autopolyploidy. The traditional approach in many plant groups, including close relatives of *Amelanchier* such *Crataegus* and *Sorbus*, is to define species broadly with multiple cytotypes. Such taxa are species only in a loose, morphological sense. Recognition of diploids as species is consistent with the bulk of our data. This does not solve the problem of semi-cryptic ploidy variation, but we think we can, with good morphological material, distinguish ploidy levels much of the time. Where there is uncertainty about distinguishing diploids and polyploids, we advocate use of species complexes, informal groups encompassing diploids and morphologically similar polyploids.

The second taxonomic challenge in *Amelanchier* apomicts is **microspecies**, groups that are morphologically uniform and often locally distributed. They are the natural outcome of diversification of newly formed apomicts. They are reproductively isolated and often distinct morphologically, and hence qualify as species according to many species concepts. They can, however, occur in great numbers and have therefore been the source of taxonomic name proliferation in many apomictic groups. Formal taxonomic status for *Amelanchier* microspecies would burden a species classification with numerous, often weakly differentiated taxa, many of which have a narrow geographic distribution.

The third taxonomic challenge in *Amelanchier* polyploids is what we call **transformed apomicts**. Successful microspecies can spread geographically as long as the habitat or habitats to which they are adapted are present. *Amelanchier* apomicts retain a little sex and, over time, variation can accrue. What started through apomictic perpetuation of morphological uniformity is transformed into heterogeneity and fuzzy boundaries of widespread apomictic polyploid groups. Many traditionally recognized *Amelanchier* species include transformed apomicts. We advocate use of species complexes for this problem.

In the spring of 2013, we made progress on our taxonomy of *Amelanchier*. The students who have worked on *Amelanchier* with me – Burgess, Cushman, and Doucette – along with Chris Frye spent a weekend together in March 2012 (our *Amelanchier* summit*)* working on an overall species classification for the genus. We have a tentative classification that we are discussing with colleagues informally, and that I presented it at the 2012 annual meeting of the American Society of Plant Taxonomists and the Botanical Society of America.

Key outcomes or Other achievements:

Our field, morphological, flow cytometric, and molecular phylogenetic studies of known *Amelanchier* diploids have created a solid foundation for understanding diversification and some of the complexity at the polyploidy level. We are translating our understanding of diversification in the genus into a classification that emphasizes three features. We want *Amelanchier* polyploid species to be cohesive, we want the classification to usable, and we want it to include as much diversity as possible.

Training of students in plant systematics is a key outcome and is described in the section, "What opportunities for training and professional development has the project provided?"

Presentations:

We have consistently presented our results at annual meetings of the American Society of Plant Taxonomists and the Botanical Society of America. Ph.D. student Eric Doucette gave a presentation at the 2013 meeting in New Orleans and another one at the 2013 Northeast Natural History Conference in Springfield, MA.

Doucette, E., K. Cushman, M. Burgess, and C. Campbell. 2013. Semi-cryptic polyploidy in *Amelanchier pallida* (Rosaceae). Presentation at the 2013 annual meeting of the American Society of Plant Taxonomists and the Botanical Society of America in New Orleans, LA; full abstract at http://www.botany.org/conferences/.

Doucette, E., K. Cushman, M. Burgess, C. Frye, and C. Campbell. 2013. Reinterpreting *Amelanchier arborea* (Rosaceae). Presentation at the 2013 annual meeting of the Northeast Natural History Conference in Springfield, MA; full abstract at http:// www.eaglehill.us/NENHC_2013/program/2013-NENHC-oral-abstracts.pdf.

Publications – We completed a treatment of *Amelanchier* for the Flora of North America, which is due to be published early in 2014. We plan to submit about nine manuscripts to refereed journals (see list below). We have not submitted any of these manuscripts yet because we needed to do extensive fieldwork to sample *Amelanchier* adequately and to assemble diverse data to help us understand diversification in the genus. We wanted a broad sample and insights from extensive field experience, morphological data, ploidy data, and DNA sequences before we craft a classification. **Earlier publication would have been premature.** Our first two publications are foundations for understanding the genus and papers that deal with individual species complexes. The first publication is an outgrowth of Michael Burgess' Ph.D. (completed in 2010) and concerns the impacts of apomixis and polyploidy on diversification and geographic distribution in *Amelanchier*. It contains over 130% more ploidy data now (1350 individuals) than we had in 2010 (580 individuals) and a far more robust sampling of the genus. The second publication focuses on diploids, and, again was a focus of Burgess' Ph.D. that we have extended significantly since 2010. Understanding diploid distribution, morphology, and phylogeny is essential for understanding polyploid apomicts. If we had published this paper in 2010, we would have not had two North American diploids that we discovered in 2010 and 2013 or the range expansion of a third diploid to include four large U.S. states in 2012.

Refereed journal papers in preparation for submission (the sequence of authors, other than the first and last authors (first author only in publication 9), is alphabetical):

1. Burgess, M., K. Cushman, E. Doucette, C. Frye, N. Talent, and C. Campbell. The impacts of apomixis and polyploidy on diversification and geographic distribution in *Amelanchier* (Rosaceae). In prep. for submission winter, 2013-2014.
2. Burgess, M., K. Cushman, E. Doucette, C. Frye, and C. Campbell. Molecular and morphological characterization of diploid *Amelanchier* species (Rosaceae). In prep. for submission in winter, 2013-2014.
3. Cushman, K., M. Burgess, E. Doucette, C. Frye, and C. Campbell,. The species problem in polyploid, apomictic *Amelanchier* (Rosaceae). In prep. for submission in spring, 2014.
4. Cushman, K., M. Burgess, E. Doucette, C. Frye, and C. Campbell. Evolution and systematics of the *Amelanchier spicata* polyploid, apomictic complex (Rosaceae). In prep. for submission in spring, 2014.
5. Burgess, M., K. Cushman, E. Doucette, C. Frye, and C. Campbell. Evolution and systematics of the *Amelanchier sanguinea* polyploid, apomictic complex (Rosaceae). In prep. for submission in summer, 2014.
6. Doucette, E., M. Burgess, K. Cushman, and C. Campbell. Evolution and systematics of the polyploid, apomictic *Amelanchier alnifolia* and *A. utahensis* complexes (Rosaceae). In prep. for submission in summer, 2014.
7. Doucette, E., M. Burgess, K. Cushman, C. Frye, and C. Campbell. Evolution and systematics of the arborescent clade of *Amelanchier* (Rosaceae). In prep. for submission in fall, 2014.
8. Doucette, E., M. Burgess, K. Cushman, and C. Campbell. Evolution and systematics of the *Amelanchier pallida* and *A. semiintegrifolia* polyploid, apomictic complexes (Rosaceae). In prep. for submission in winter, 2014.
9. Campbell. C., M. Burgess, K. Cushman, E. Doucette, and C. Frye. A monograph of *Amelanchier* (Rosaceae). In prep. for submission in spring, 2015. This monograph will be maintained, with online keys and images, on our *Amelanchier* website (http://biology.umaine.edu/Amelanchier/).

*** What opportunities for training and professional development has the project provided?**

Three graduate students have been involved in all phases of this project, including fieldwork, labwork, various analyses of phylogeny and morphology, understanding literature pertinent to the project, botanical nomenclature, and grappling with the challenges of classifying an apomictic group. Michael Burgess completed his Ph.D. at the University of Maine in 2010 and has a tenure-track position at the State University of New York, Plattsburgh. Eric Doucette has completed his comprehensive exams and is now a Ph.D. candidate at the University of Maine, and Kevin Cushman is nearing completion of an M.S. at the University of Maine. Both Doucette and Cushman are working on *Amelanchier*. Like Burgess, they have individual projects and are collaborating on each other's publications. All these students have given presentations on *Amelanchier* at annual meetings of the American Society of Plant Taxonomists and the Botanical Society of America. They participated in a weekend-long *Amelanchier* summit in March 2012, along with our collaborator, Chris Frye, Maryland Department of Natural Resources. We discussed our progress on this project and our approach to classifying the species of *Amelanchier*. They are scheduled to meet with workers in two other taxonomically challenging groups in the Rosaceae, *Crataegus* and *Rubus*, in March 2014 to discuss taxonomic challenges and solutions.

These students also received extensive training in using herbaria by working in herbaria at the Gray Herbarium. New York Botanical Garden, Philadelphia Academy of Science, University of Maine, and University of British Columbia.

Several undergraduates have been involved in this project, including two who completed senior theses on *Amelanchier*, Kevin Cushman and Gretchen Nelson. Undergraduates have had less intense and narrower training, but Cushman and Nelson (who both received a B.S. in Botany at the University of Maine) did their senior theses on *Amelanchier*, and they presented posters on their senior thesis research at annual meetings of the American Society of Plant Taxonomists and the Botanical Society of America.

Kevin Cushman is currently planning to apply to graduate programs in plant genetics at several North American universities, and I am strongly supporting his application.

*** How have the results been disseminated to communities of interest?**

There are two communities of primary interest to us. The first are botanists, horticulturists, wildlife ecologists, conservation biologists, land-use managers, and others who work with *Amelanchier*. We want our classification to be usable for them. In the spring of 2013, former Ph.D. student Burgess, Ph.D. student Doucette, and PI Campbell gave presentations and/or workshops to mostly field botanists about taxonomic challenges in *Amelanchier* (see output). This is important in terms of getting feedback about our taxonomic approach. PI Campbell gave the 2013 New England Botanical Club (NEBC) distinguished speaker lecture on *Amelanchier* and emphasized what we know about diversification in the genus, the three challenges to classification (semi-cryptic ploidy variation, microspecies, and transformed apomicts), and a draft species classification for eastern North America. Feedback from NEBC was that our insights into *Amelanchier* diversification made them appreciate more the complexity in the genus and difficulties in classifying it. They liked the use of species complexes where taxon boundaries are uncertain.

Products

Books

Book Chapters

Conference Papers and Presentations

Doucette, E., K. Cushman, M. Burgess, C. Frye, and C. Campbell (2013). *Reinterpreting Amelanchier arborea (Rosaceae)*. annual meeting of the Northeast Natural History Conference. Springfield, MA. Status = PUBLISHED; Acknowledgement of Federal Support = Yes

Doucette,,E., K. Cushman, M. Burgess, and C. Campbell (2013). *Semi-cryptic polyploidy in Amelanchier pallida (Rosaceae)*. annual meeting of the American Society of Plant Taxonomists and the Botanical Society of America. New

Orleans, LA. Status = PUBLISHED; Acknowledgement of Federal Support = Yes

Inventions

Nothing to report.

Journals

Licenses

Nothing to report.

Other Products

Nothing to report.

Other Publications

Campbell, C.S., M.B. Burgess, K.R. Cushman, E.T. Doucette,. A.C. Dibble, and C.T. Frye (2014). *Amelanchier in FNA Editorial Committee, Flora of North America volume 9. Magnoliophyta: Rosidae (in part): Rosales (in part).*. Invited, peer-reviewed taxonomic treatment of Amelanchier for the Flora of North America. Status = AWAITING_PUBLICATION; Acknowledgement of Federal Support = Yes

Patents

Nothing to report.

Technologies or Techniques

Nothing to report.

Thesis/Dissertations

Websites

Nothing to report.

Participants/Organizations

Research Experience for Undergraduates (REU) funding

Form of REU funding support:	REU supplement
How many REU applications were received during this reporting period?	Nothing to Report
How many REU applicants were selected and agreed to participate during this reporting period?	Nothing to Report
REU Comments:	We did have one REU previous to this reporting period.

What individuals have worked on the project?

Name	Most Senior Project Role	Nearest Person Month Worked
Campbell, Christopher	PD/PI	4
Burgess, Michael	Faculty	1

Cushman, Kevin	Graduate Student (research assistant)	3
Doucette, Eric	Graduate Student (research assistant)	3

Full details of individuals who have worked on the project:

Christopher S Campbell
Email: campbell@maine.edu
Most Senior Project Role: PD/PI
Nearest Person Month Worked: 4

Contribution to the Project: Overall direction of the project; advising graduate students working on the project; also fieldwork, data collection, data analysis, writing manuscripts,

Funding Support: Full-time faculty at the University of Maine

International Collaboration: No
International Travel: Yes, Greece - 0 years, 0 months, 7 days; Spain - 0 years, 0 months, 7 days; Canada - 0 years, 0 months, 1 days

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Michael Burgess
Email: michael.b.burgess@plattsburgh.edu
Most Senior Project Role: Faculty
Nearest Person Month Worked: 1

Contribution to the Project: Data analysis and writing manuscripts.

Funding Support: Dr. Burgess, former Ph.D. student at the University of Maine, is tenure-track faculty at SUNY Plattsburg.

International Collaboration: No
International Travel: No

Kevin Cushman
Email: kevin.cushman@umit.maine.edu
Most Senior Project Role: Graduate Student (research assistant)
Nearest Person Month Worked: 3

Contribution to the Project: Fieldwork, data collection, data analysis, participation in manuscript preparation.

Funding Support: Teaching assistant at the University of Maine

International Collaboration: No
International Travel: Yes, Canada - 0 years, 0 months, 14 days

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Eric Doucette
Email: eric_doucette@umit.maine.edu
Most Senior Project Role: Graduate Student (research assistant)
Nearest Person Month Worked: 3

Contribution to the Project: Fieldwork, data collection, data analysis, participation in manuscript preparation

Funding Support: Teaching assistant at the University of Maine

International Collaboration: No
International Travel: No

What other organizations have been involved as partners?
Nothing to report.

What other collaborators or contacts have been involved?

YES

Impacts

What is the impact on the development of the principal discipline(s) of the project?

Species are fundamental units in biology, and nowhere in plants is the delimitation of species more difficult than in apomictic groups. Hybridization, polyploidy, and apomixis each may confound species-level taxonomy, and these forces combine in agamic complexes to create intricate patterns of variation. *Amelanchier* is a prominent North American genus and has long challenged systematists. There is sharp disagreement about species among the major taxonomic treatments of the genus. A usable, sound classification of the species of *Amelanchier* is therefore important for botanists, horticulturists, wildlife ecologists, conservation biologists, land-use managers, and others.

We now have tools to see more clearly into the history of diversification in *Amelanchier*. We are assembling abundant data about morphological variation, estimating ploidy level with flow cytometry, inferring reproductive mode with studies of seed ploidy level, and testing phylogenetic relationships based on DNA sequence. We are building a broadly based approach to delimiting species with data from morphology, molecular phylogeny, ploidy level, reproductive mode (sexual or apomictic), geography, habitat preferences, and flowering time. Our insights into diversification of polyploidy apomicts, methodology, and taxonomic approach may be applicable to other apomictic groups.

What is the impact on other disciplines?

Because *Amelanchier* is a prominent genus, especially in North America, where it is native in every state of the United States except Hawaii and most Canadian provinces, a usable, sound classification of the species of *Amelanchier* is important for botanists, horticulturists, wildlife ecologists, conservation biologists, land-use managers, and others. We aim to provide a sound taxonomic classification of the genus.

What is the impact on the development of human resources?
Nothing to report.

What is the impact on physical resources that form infrastructure?
Nothing to report.

What is the impact on institutional resources that form infrastructure?
Nothing to report.

What is the impact on information resources that form infrastructure?
Nothing to report.

What is the impact on technology transfer?

Nothing to report.

What is the impact on society beyond science and technology?

Amelanchier is of some importance as a minor fruit crop (Canada in especially) and is used as a landscape planting. Our papers and monograph may contain information that could be useful for people involved in these uses of this genus. For example, knowledge of the geographic distribution could be informative about cold hardiness. Our descriptions of taxa may suggest qualities, such as flower size, that could be important horticulturally.

Changes/Problems

Changes in approach and reason for change

Our original proposal included a workshop on pollination biology to K-12 teachers. We have not done this, but instead have given presentations to the public about taxonomic challenges in *Amelanchier.*

Actual or Anticipated problems or delays and actions or plans to resolve them

Nothing to report.

Changes that have a significant impact on expenditures

Nothing to report.

Significant changes in use or care of human subjects

Nothing to report.

Significant changes in use or care of vertebrate animals

Nothing to report.

Significant changes in use or care of biohazards

Nothing to report.