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PERSPECTIVES AND PARADIGMS

Evidence does not support the targeting of cryptic invaders at the subspecies level using classical biological control: the example of *Phragmites*

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Abstract Classical biocontrol constitutes the importation of natural enemies from a native range to control a non-native pest. This is challenging when the target organism is phylogenetically close to a sympatric non-target form. Recent papers have proposed and recommended that two European moths (*Archanara* spp.) be introduced to North America to control non-native *Phragmites australis australis*, claiming they would not adversely affect native *P. australis americanus*. We assert that these papers overlooked research contradicting their conclusions and that the authors recommended release of the non-native moths despite results of their own studies indicating that attack on native *Phragmites* is possible after field release. Furthermore, their open-field, host-specificity tests were conducted in non-wetland fields in Switzerland using potted plants, reflecting considerably different conditions than those of North American wetlands. Also, native *Phragmites* in eastern North America has declined, increasing its potential vulnerability to any

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new stressors. Because all inadvertently introduced, established, *Phragmites*-specialist, herbivorous insects have done more harm to native than non-native *Phragmites*, native *Phragmites* may experience more intense herbivory than non-native *Phragmites* from the introduction of *Archanara* spp. due to demographic mechanisms (e.g., increase in density of the biocontrol agent and spillover onto alternate hosts) or because the herbivores may undergo genetic change. In addition to the risk to native *Phragmites,* significant biomass reduction of non-native *Phragmites* may decrease important ecosystem services, including soil accretion in wetlands affected by sea level rise. We strongly caution against the approval of *Archanara* spp. as biocontrol agents for non-native *Phragmites* in North America.

Keywords Ecosystem services · Herbivory · Host switching · Invasive species · Non-target impacts of biocontrol · *Phragmites australis*

Introduction

There has been controversy for many years about the risks of classical biological control to non-target species (Simberloff and Stiling 1996), although, during this period, biocontrol has progressed to a modern and circumspective science heralding numerous successes (Heimpel and Cock 2018). In the age of globalization, biological control practitioners are not only challenged by the dramatic increase in occurrence of non-native species (Meyerson and Mooney 2007; Stohlgren et al. 2011) but also by discoveries of “cryptic invaders” (non-native species, hybrids, or genotypes that cannot be easily distinguished from native species or genotypes; Gaskin and Schaal 2002; Saltonstall 2002; Ciotir et al. 2013). As we show in this paper, finding an effective biological control agent with the specificity to negatively affect only the targeted cryptic invader is a daunting task, especially given their genetic, morphological, or physiological similarity to native species or genotypes.

The classical biological control program aimed at non-native *Phragmites* has been in development for 20 years (Blossey and McCauley 2000) and has been controversial for almost as long (Rooth and Windham 2000; Meyerson et al. 2009; Packer et al. 2017). The Old World or “European” form of *Phragmites australis* [called *P. australis* subsp. *australis* or “non-native *Phragmites*” to distinguish it from the native American *P. australis* subsp. *americanus* or “native *Phragmites*” (Saltonstall et al. 2004)] is an invasive plant in the United States and Canada and has been the target of widespread management efforts for more than 40 years (Hazelton et al. 2014).

Recently, Casagrande et al. (2018) advocated for biological control programs that target cryptic invaders at the subspecific level. To support their argument, they presented the case of *Phragmites australis* (Cav.) Trin. ex Steud. (hereafter *Phragmites*) in North America, in which a highly invasive, non-native lineage broadly overlaps and interbreeds with other native and non-native lineages (Lambertini et al. 2012; Meyerson et al. 2012; Saltonstall et al. 2014, 2016; Wu et al. 2015; Williams et al. 2019). Although there has never been a documented case of successful biological control of a weed at the subspecific level, Casagrande et al. (2018) suggested that it is possible because some biocontrol herbivores can exhibit such specificity. In particular, Blossey et al. (2018a), conducted greenhouse, laboratory, and open-field, host-specific trials on acceptance, larval growth, and oviposition by two European moth species on *Phragmites*. Many of their studies showed no differences between non-native and native *Phragmites*, but, in some, they observed reduced survival (by 40–50% in no-choice studies) and oviposition rates (on 6.5% of eggs laid in an open-field test with one-third of the plants being native *Phragmites* and the other two-thirds American or European non-native *Phragmites*) on native *Phragmites*. These findings were the basis for their conclusion that “*P. australis americanus* genotypes are within the physiological or fundamental host range of *A. geminipuncta* and *A. neurica*” and their decision to “recommend release of these two biocontrol agents in North America.”

In this paper we review the available data and draw the opposite conclusion, namely that biological control of non-native *Phragmites*, and, more generally, any case of biological weed control at the subspecific level, remains a risky endeavor. We discuss the

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literature regarding the biological control of non-native *Phragmites* in North America and the potential intended and unintended consequences if such a program were to be instituted. As we detail below, Casagrande et al. (2018) have downplayed the role that evolution can have on the adoption of new genotypes, subspecies, or species into an herbivore's diet. Moreover, they have not addressed the indirect species interactions (e.g., spillover effects and apparent competition) that operate at larger scales than can be tested in simple laboratory settings. Blossey et al. (2018a) have also acknowledged that, despite years of extensive host-specificity testing, they "cannot categorically exclude the possibility of attack on *P. australis americanus* after field release." Focusing on *Phragmites* specifically, there are additional issues at play, including the occurrence of other *Phragmites* lineages and hybrids in North America (see Saltonstall 2002; Lambertini et al. 2006, 2012; Lambertini 2016; Meyerson et al. 2012; Saltonstall et al. 2014; Packer et al. 2017 for a full review of *Phragmites* lineages and genotypes in North America). Conserving infraspecific (below the species level) genetic diversity is important for, among other reasons, its role in facilitating ecological processes such as trophic cascades (Des Roches et al. 2018). Further, non-native *Phragmites* has important societal benefits in some regions of the United States and native *Phragmites* has cultural significance—all of these are at risk if biological control agents targeting non-native *Phragmites* are introduced. Native *Phragmites* has declined in the eastern U.S. (Saltonstall and Stevenson 2007; Meyerson et al. 2010b), increasing its potential vulnerability to additional stressors. Finally, while it is not our intent to repeat previously published criticisms of *Phragmites* biocontrol (Bhattarai et al. 2016; Cronin et al. 2016) or the responses (Blossey and Casagrande 2016a, b), these publications were not cited by Casagrande et al. (2018) so we will reiterate some of the key elements here.

Evolution and ecology of novel interactions

Certainly, there have been relatively few documented cases of significant non-target attacks from biological control agents (van Klinken and Edwards 2002; Suckling and Sforza 2014; Wright and Bennett 2018). However, the number of documented cases is likely to be an underestimation for several reasons: the monitoring of non-target species has been minimal historically (Simberloff and Stiling 1996), there may be a post-introduction lag phase before density-dependent host range expansion and coevolution, and we are aware of no prior biocontrol programs at the subspecific level. In other words, there are few data from which to estimate non-target attack rates. Furthermore, the arguments of Casagrande et al. (2018) (e.g., phylogenetic conservatism of host range) are almost all based on interspecific or higher taxonomic-level comparisons. This precludes consideration of the *infra*specific variation that already complicates management of *Phragmites* and which only increases the likelihood that any introduced biological control agent would adopt the native *Phragmites* lineage into its host range. It is also important to note that the proposed biological control agents, *Archanara geminipuncta* (Haworth) and *A. neurica* (Hübner) (Lepidoptera: Noctuidae), are not specialists but are oligophagous on multiple *Phragmites* lineages and other wetland grasses, including some economically important species (Blossey et al. 2013, 2018a; Blossey 2014). Thus, a major concern remains about the *Phragmites* biological control program, namely that any introduced herbivores may form novel and damaging host associations with native *Phragmites* or other non-target species.

Casagrande et al. (2018) downplayed the ecological and evolutionary processes that underlie the incorporation of novel host species or genotypes into the host range in the wild. Such novel interactions can form in two main ways: ecological fitting or evolution. Ecological fitting describes the formation of novel species interactions as a result of pre-existing traits (e.g., phenology, palatability, defenses) but with no coevolutionary history. Such novel interactions have been observed across many taxa, trophic levels, and systems, with two of the better-known examples being California butterflies using non-native larval hosts (Graves and Shapiro 2003) and leaf chewers and miners feeding on introduced oaks (Pearse and Hipp 2009). Ecological fitting has also been reported for two major pests of forest trees, the emerald ash borer (*Agrilus planipennis* Fairmaire) (Cipollini and Peterson 2018) and the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Erbilgin et al. 2014). Several biological control agents themselves are examples, such as *Rhinocyllus conicus* Frölich on native thistles

(Louda et al. 2003) and *Chrysolina quadrigemina* (Suffrian) on non-target, native and non-native *Hypericum* spp. (Andres 1985). Interestingly, novel interactions can often be predicted from phylogeny, because the host range of insect herbivores generally shows a strong phylogenetic signal (Pearse and Hipp 2009; Pearse et al. 2013; Gilbert et al. 2015; Parker et al. 2015). In other words, introduced herbivores are more likely to incorporate plants into their host ranges that are closely related to their original hosts. However, not all traits involved in ecological fitting will be phylogenetically conserved (e.g., ecophysiological traits; Desurmont et al. 2011; Whitfeld et al. 2012; Erbilgin et al. 2014; Cipollini and Peterson 2018). Thus, it is important to assess these traits in combination with phylogeny, which has led to innovative and successful approaches to predicting novel interactions (e.g., Pearse and Altermatt 2013). Moreover, theoretical and empirical research has demonstrated that the likelihood of host range expansion increases at high population densities of the natural enemy in question, and when primary and alternate hosts co-occur (Araujo et al. 2015; Castagneyrol et al. 2016). Finally, one research area yet to be addressed for *Phragmites* but previously identified as important (Blossey 2014) concerns the potential for *Archanara* moths to be incorporated into the diet of natural enemies (e.g., predators and parasitoids). Such an interaction could reduce their efficacy, have indirect effects on non-target species (Pearson and Callaway 2005), or even promote feeding on native *Phragmites*. This may provide 'enemy free space' as it does for other internal stem feeders such as *Lipara* Meigen spp. (Diptera: Chloropidae) (Allen et al. 2015).

Evolution can also contribute to the formation of novel interactions and has been previously identified as the greatest risk to non-target species in weed biological control by some in the field (van Klinken and Edwards 2002). Indeed, rapid evolution has frequently occurred in species introduced to a new range (e.g., Maron et al. 2004; Prentis et al. 2008; Buswell et al. 2010; Turner et al. 2014; Stutz et al. 2018). This includes *Phragmites* (Guo et al. 2014, 2018; Cronin et al. 2015) as well as a number of biological control agents (Szűcs et al. 2012). However, the evolution of novel interactions is more challenging to demonstrate, with the best-known example being unrelated to biocontrol, namely that of soapberry bugs (*Jadera haematoloma* Herrich-Schäffer) (Hemiptera: Rhopalidae), which evolved different length mouthparts to incorporate multiple introduced plant species into their host range (Carroll and Boyd 1992; Dingle et al. 2009; Cenzer 2016). In the case of the proposed biocontrol agents for *Phragmites*, *A. geminipuncta* and *A. neurica*, the native lineage of *Phragmites* is already known to be within the physiological and fundamental host range of both species (Blossey et al. 2018a). Because *Archanara* spp. already feed on several other plant species (e.g., in host range testing) as a result of ecological fitting (Blossey et al. 2013, 2018a; Blossey 2014), a major barrier has already been crossed. The only evolutionary step remaining for *Archanara* to shift to native *Phragmites* is that of changes in patterns of fundamental host use, which could be driven by high population density, decreasing frequency of the primary host (i.e., non-native *Phragmites*), and increasing relative frequency of potential alternate hosts (i.e., native *Phragmites*) (Murdoch 1969). Combining these demographic characteristics with the multiple phylogenetically and functionally similar non-target hosts that co-occur spatially and temporally with non-native *Phragmites*, and given that native *Phragmites* is within the fundamental host range of both *Archanara* species, it is entirely possible that the proposed biological control agents will evolve to be more effective against the non-target, native *Phragmites*. That said, we recognize that predicting post-introduction evolutionary trajectories remains a major challenge in ecology. Furthermore, potential also exists for non-native *Phragmites* to evolve resistance to the proposed biocontrol agents, especially given the novel admixture of genetic diversity present in North America (reviewed by Meyerson et al. 2012), high prevalence of sexual reproduction (McCormick et al. 2010), and the demonstrated rapid evolution in plant defenses of the non-native lineage (Cronin et al. 2015; Allen et al. 2017a, b; Bhattarai et al. 2017a). Such a phenomenon has received little consideration to date but has been observed in Canada with purple loosestrife (*Lythrum salicaria* L.), which has evolved resistance to its beetle biological control agent *Neogalerucella calmariensis* (L.) (Coleoptera: Chrysomelidae) (Stastny and Sargent 2017), as well as for the Argentine stem weevil (*Listronotus bonariensis*) (Kuschel) (Coleoptera: Curculionidae) and its (now ineffective) parasitoid *Microctonus hyperodae*

Loan (Hymenoptera: Braconidae) in New Zealand (Tomasetto et al. 2018).

Herbivory on *Phragmites australis* lineages in North America

The identity of *Phragmites* herbivores and the ecological and evolutionary consequences of herbivory are well-studied for all major lineages of the species in North America (e.g., Tewksbury et al. 2002; Lambert and Casagrande 2007; Lambert et al. 2007; Park and Blossey 2008; Saltonstall et al. 2014; Allen et al. 2015, 2017a, b; Cronin et al. 2015; Bhattarai et al. 2017a, b). A great majority of these herbivores include exotic specialist and semi-specialist species that were co-introduced to North America from their native ranges in Europe and Asia. All the introduced species that were specialists on the non-native *Phragmites* have apparently expanded their niches to include the native and Gulf Coast lineages of *Phragmites* in North America (Tewksbury et al. 2002; Blossey 2003; Lambert and Casagrande 2007; Lambert et al. 2007; Allen et al. 2015; Cronin et al. 2015). These cases strongly contradict the assertion of subspecies-level host-specificity of *Phragmites* herbivores. Although Blossey and Casagrande (2016a, b) and Casagrande et al. (2018) consider *Lipara pullitarsis* Doskocil and Chvala (Diptera: Chloropidae) as an example of subspecies-level host specificity, evidence of infestation on native plants has been documented by Allen et al. (2015). Another species accidentally introduced from Europe, *Lasioptera hungarica* Möhn (Diptera: Cecidomyiidae), purported to be a specialist of non-native *Phragmites*, has been shown to feed on the hybrids of native and non-native lineages in the field (Saltonstall et al. 2014). For this and other species that exhibit a strong preference for the non-native lineage, the hybrid may serve as a bridge to native *Phragmites* (see Floate and Whitham 1993). Furthermore, plants of the native lineage are more palatable to a wide range of herbivores than plants of the non-native lineages (Allen et al. 2015; Cronin et al. 2015, 2016; Bhattarai et al. 2017a). These two key pieces of evidence, higher palatability of native *Phragmites* and an overwhelming record of host range expansion by the specialist herbivores of non-native *Phragmites* to include the native *Phragmites*, strongly suggest that the native lineage would be a highly susceptible naïve host to any new herbivores introduced to North America. Consequently, native *Phragmites* could experience the negative effects of spillover, associational susceptibility, and apparent competition if *Archanara* spp. were introduced as biocontrol agents. A recent study by Bhattarai et al. (2017b) supported this prediction, demonstrating strong apparent competition, mediated by three herbivore guilds, that disproportionately affected the native lineage. Interestingly, two of the herbivore guilds (a sucking insect [the aphid *Hyalopterus pruni,* (Geoffroy)] and gall-forming insects [*Lipara* spp.]) that mediated apparent competition involved introduced species (Bhattarai et al. 2017b). Such a possibility remains to be tested with *Archanara* spp.

Casagrande et al. (2018) stated that larvae of *Archanara* spp. could not survive through winter on native *Phragmites* because they oviposit beneath leaf sheaths, which typically abscise in autumn, whereas leaf sheaths of non-native *Phragmites* tend to persist through winter and thus offer greater protection. In fact, loose leaf sheaths are a typical but variable trait of native *Phragmites*, which is why using it as an identifying characteristic has given way to genetic analysis in cases where lineage needs to be determined unequivocally (Saltonstall 2003c; Tulbure et al. 2012; Guo et al. 2014). Some native populations retain leaf sheaths to a greater degree than others and Allen et al. (2017a, b) and Swearingen and Saltonstall (2012) have cautioned that morphological and phenological traits are subtle, sometimes subjective, and variable across the North American range of *Phragmites*. Moreover, Blossey et al. (2018a) found that leaf abscission in autumn less than halved larval attack rates of stems the next spring and did not eliminate the *Archanara* population entirely.

Research involving proposed biocontrol agents

Classical biological control programs often undergo a rigorous evaluation of intended and unintended consequences of proposed biocontrol agents in the introduced range. In the case of *Phragmites* and the proposed biocontrol agents *A. geminipuncta* and *A. neurica*, there is a paucity of scientific evidence (1) demonstrating the efficacy of those insects in controlling non-native *Phragmites* in North America and (2) ensuring that there will be no negative consequences to the members of natural ecosystems and agricultural areas. To the best of our knowledge, there has been no publication demonstrating the impact of either of those herbivores on growth, performance, and population dynamics of non-native *Phragmites* in North America. The only study presented in the context of biological control was a field survey and a common garden experiment evaluating *Archanara* damage on non-native *Phragmites* in its native range in Switzerland (Häfliger et al. 2006). However, evolutionary changes of invasive plants in response to the novel environment (both biotic and abiotic) of the introduced range render those results less robust to predict their success in controlling invasive plants. In its non-native range, *P. australis australis* exhibits stronger defense responses against herbivores through leaf toughness, total phenolics, and nutrient concentrations (% C and N in leaf tissues) than in its native range (Cronin et al. 2015). Rigorous studies evaluating the impact of *Archanara* spp. on the performance, growth, and expansion of populations of non-native *Phragmites* are necessary before assessing whether they are worthy of consideration as biological control agents.

Furthermore, assessments of potential biocontrol introductions need to provide evidence that they do not have negative consequences for members of natural ecosystems and agricultural areas, and such evidence has not been presented for *Archanara* spp. in North America. Contrary to the expectation of specificity at the subspecies level, these species are not specialists, even at the genus level. In addition to both species consuming and ovipositing on native *Phragmites*, both species fed on several other species of wetland plants and economically important crops (Blossey et al. 2013, 2018a). Of 43 non-*Phragmites* species examined, *A. geminipuncta* was shown to feed on 9 species in no-choice tests including *Arundinaria tecta* (Walter) Muhl., *Arundo donax* L., *Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn., *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller, *Spartina alterniflora* Loisel., *S. cynosuroides* L. (Roth), *Zizania aquatica* L., and the commercial crop species rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.) (Blossey et al. 2013, 2018a: Tables 1 and 2, respectively). Similarly, *A. neurica* fed on 7 species, namely *Eragrostis trichodes* (Nutt.), *Phalaris arundinacea* L., *Schoenoplectus acutus* (Muhl. ex J.M.Bigelow) Á. Löve and D. Löve, *S. alterniflora*, *Z. aquatica*, *Glyceria striata* (Lam.) Hitchc., and sugarcane (*Saccharum officinarum* L.). Moreover, first instar larvae of both *Archanara* species survived on several of the test species (*S. alterniflora*, *S. cynosuroides*, *Cortaderia selloana*, *Oryza sativa*, and *Schoenoplectus acutus*) for the two week duration of the experiment (Blossey et al. 2018a; Table 3). Although the concerns over these results (e.g., Bhattarai et al. 2016; Cronin et al. 2016) have been dismissed as unimportant damage in no-choice experiments (Blossey and Casagrande 2016b), these results are critical in evaluating potential harmful ecological and economic consequences of the biocontrol agents through indirect effects (Simberloff 2012). Paynter et al. (2015) analyzed data from no-choice feeding and oviposition tests performed for arthropod agents in New Zealand and concluded that these tests were an efficient means of predicting if non-target species would experience serious damage. However, Paynter et al. presented an example of testing that failed to predict extensive damage to a native thistle by a weevil distributed to target *Cirsium arvense* (L.) Scop., and cautioned that the twelve cases they had analyzed may have had insufficient replication of tests to yield robust conclusions. Given the current lack of evidence, the introduction and release of *Archanara* spp., which are known to feed on multiple native plant species and economically important crops, should be postponed until further evidence is acquired. Moreover, several of the potential alternate plant hosts identified by Blossey et al. (2013)—*S. alterniflora, Z. aquatica,* and *Schoenoplectus americanus*—are foundation species in coastal and inland marsh restoration efforts. Such projects cost many millions in taxpayer dollars annually and restore critical ecosystem services to coastal residents, fisheries, and other wildlife (Barbier et al. 2011). A quantitative assessment of the potential effects that releasing any biological control agent could have should be undertaken to identify intended and unintended consequences.

After acknowledging the lack of host specificity, the solution proposed by Casagrande et al. (2018) and Blossey et al. (2018a) to infestation of native *Phragmites* by *Archanara* spp. was mowing and burning *Archanara*-infested stands. Given that mowing and burning are practices employed by land managers to contain or weaken non-native *Phragmites* (Hazelton et al. 2014 and citations within), exposure of native *Phragmites* to multiple stressors (biocontrol plus mowing or burning) could decimate native lineages.

This approach is also impractical where the use of fire could threaten residential areas.

On a practical level, we agree with Blossey et al. (2018a) that open-field host-specificity tests are more realistic than those conducted in the lab, greenhouse, or outdoor cages. Nonetheless, the condition of test plants and the growing environment are critical to the realism of field trials (USDA 2016), yet a common problem in open-field trials is the suboptimal growth of non-target plants that are not typically cultivated (Schaffner et al. 2018). The attack on positive controls (i.e., *Phragmites australis*) found by Blossey et al. (2018a, b) demonstrated that conditions were suitable for the biocontrol agent but did not demonstrate that non-target plants experienced conditions similar to those of natural wetlands. The open-field tests used pot-grown plants, which are highly susceptible to nutrient or water stress (USDA 2016). Moreover, the soil type and fertilization regime were not described for the experiment (Blossey et al. 2018a, b), and it is not mentioned (and therefore unlikely) that native *Phragmites* pots were supplemented with reduced iron. In pot cultivation, it is important to alleviate iron limitation and its associated effects like chlorosis and growth reduction (Willson et al. 2017). Further, the pots were placed in a mown, non-wetland field, creating a drained hydrologic condition that would have further decreased the availability of reduced iron and could have thereby altered plant physiological processes. It is thus possible that the growth problems resulting in thin stems of *P. a. berlandieri* reported by Blossey et al. (2018a) were due to suboptimal soil, fertility, or moisture conditions rather than climate. The abundance of host plant species relative to the non-target plants can also influence test outcomes; in designs where host plant abundance is greater than that of non-target plants, the likelihood of non-target plants being attacked decreases (Schaffner et al. 2018). Native *Phragmites* comprised only one-third of the plants used in the open-field tests of Blossey et al. (2018a, b), with the other two-thirds being plants of European and North American non-native *Phragmites*. Thus, the result that both moth species only laid 6.5% of eggs on native *Phragmites* should be considered in light of two considerations: (1) high host plant densities may have inhibited searching behavior of herbivores (Schaffner et al. 2018) and (2) egg-laying on native *Phragmites* would have been 33% even if egg-laying was identical across the three groups tested.

Based on our evaluation of the literature, our position is that several critical questions must be explicitly addressed before any biological control agent for non-native *Phragmites* could be safely approved for release in North America:

1. What are the expected geographic and ecological range limits for the proposed biocontrol agents in North America?
2. What are the impacts of the proposed biocontrol agents on the growth, performance, and population dynamics of non-native *Phragmites*?
3. What is the potential for negative non-target impacts by the proposed biocontrol agents, both behavioral (i.e., apparent competition) and evolutionary (i.e., genetic host switches)?
4. How likely are native and non-native *Phragmites* to evolve resistance to the proposed biocontrol agents?
5. What potential natural enemies do the proposed biological control agents have in North America, how do these vary geographically, and what indirect effects may be predicted from this knowledge?
6. How do the answers to the above questions vary among the major lineages, haplotypes, and hybrids present in North America?
7. If non-target impacts appear unavoidable, what is the relative risk of biological control vs. other management approaches in terms of the fate of the native *Phragmites* lineage?

Genetics

Both the native and non-native populations of *Phragmites* in North America exhibit high genetic and genomic diversity (Saltonstall 2002, 2003a; Saltonstall et al. 2010; Lambertini et al. 2006, 2012; Lambertini 2016; McCormick et al. 2010; Meyerson et al. 2010a, b, 2012, 2016a, b; Meyerson and Cronin 2013; Kulmatiski et al. 2011; Kettenring and Mock 2012; Colin and Eguiarte 2016). The native *Phragmites* is often referred to as a single lineage when contrasted with the non-native Old World lineage, but it includes 17 distinct haplotypes that have different distributions and range sizes in North America. These native haplotypes have different genetic distances among them and with the introduced lineage (Saltonstall 2003b; Lambertini 2016). This might imply large and still unexplored variation in the response to the proposed biocontrol agents. The western states are a center of diversity for native *Phragmites*, and native populations can be genetically very different even at the local scale (Kettenring and Mock 2012). This large genetic and geographic variation has not been considered in the laboratory host preference trials, which comprised up to three genotypes per lineage (Blossey et al. 2013). This subset is unlikely to represent the wide range of genetic, morphologic, and physiologic variation, as well as variation of environments, in North America. Moreover, other native, potentially endangered, *Phragmites* populations were recently discovered in México (Colin and Eguiarte 2016), where biocontrol could spread from the United States.

In addition, hybridization between native and non-native lineages has been detected in multiple studies (Meyerson et al. 2010a; Paul et al. 2010; Saltonstall et al. 2014, 2016; Wu et al. 2015; Lambertini 2016). The occurrence and impacts of hybrids in populations should not be underestimated, as has been shown with hybrid complexes of a number of other plant species. Hybrids may be “sinks” for insects and divert the biocontrol from its target (Floate et al. 1993; Williams et al. 2014). On the other hand, hybrids could escape the biocontrol and replace the non-native populations. For example, Hallgren et al. (2003) found that phenolic compounds decreased with increasing introgression in *Salix* hybrids. In *Tamarix* spp., introgression increased with latitude and was highly correlated with resistance to insect attack (Williams et al. 2014). Hybrids may also have a different phenology from their parents and increase the fecundity of the herbivore by setting leaves earlier in the spring (Floate et al. 1993). In one case, grazing geese ignored *Spartina* hybrids and preferentially consumed native plants, contributing to the expansion of the hybrid invasive populations in a California estuary (Grosholz 2010). These findings indicate that hybridization and introgression play an important role in structuring herbivore communities. This aspect has not been considered in the studies of host specificity for the biocontrol of *Phragmites.*

Ecosystem services provided by *Phragmites*

The negative impacts of non-native *Phragmites* in North America are well-documented (Packer et al. 2017 and references within). However, *Phragmites* also provides many ecosystem services in North America (Hershner and Havens 2008; Kiviat 2013). These services prominently include nutrient sequestration in eutrophic environments (Meyerson et al. 2000; Mozdzer et al. 2010), phytoremediation of heavy metals and nutrients (Meyerson et al. 2000; Windham et al. 2003), protection of coastal soils from storms and enabling marshes to better keep up with sea level rise (Windham and Lathrop 1999; Rooth and Stevenson 2000; Rooth et al. 2003; Ravit et al. 2015; Knight et al. 2018), carbon sequestration (Caplan et al. 2015), providing faunal habitat (Kane 2001; Weis and Weis 2003; Kiviat 2013), enabling the continuation of cultural uses by Native Americans (Kiviat and Hamilton 2001; Long et al. 2003), and widespread use for sewage treatment and sludge dewatering (Begg et al. 2001; Rodríguez and Brisson 2015). Most of these services are due to non-native *Phragmites*, although the cultural uses by Native Americans are at least partly due to native *Phragmites*. An especially important example of soil stabilization exists on the Louisiana coast where a recently flourishing, non-native scale insect is devastating large expanses of *Phragmites* and causing marsh collapse (Knight et al. 2018). Although *Phragmites* is invasive in coastal habitats, it may be one of the few species capable of keeping pace with accelerating sea level rise, though there is some evidence that it can also accelerate carbon loss (Bernal et al. 2016 but see Kirwan et al. 2016). If *Archanara* spp. were to remove substantial biomass from non-native *Phragmites*, a number of the aforementioned ecosystem services would be adversely affected. In particular, if high-density stands experienced widespread mortality, the belowground structure of wetlands may become destabilized and collapse, allowing the wetland to become permanently inundated.

Biocontrol generally reduces weed biomass substantially (Stiling and Cornelissen 2005). Classical biocontrol tends to be spatially nonselective, and, if the proposed biocontrol program is established, may greatly reduce the aboveground and belowground *Phragmites* biomass and structure that supports ecosystem services. The architecture of *Phragmites* stands after being affected by biocontrol is unpredictable and might not support the biodiversity and other desirable services now supported by non-native *Phragmites*. For example, reduced aboveground or belowground biomass might lessen the protection of tidal marsh sediments; shorter or more slender culms might provide less sturdy nest substrate for marsh wrens (*Cistothorus palustris* Wilson); and lack of seed production might affect the food supply of certain migrant or wintering songbirds (see Kiviat 2013 and references within). Native *Phragmites*, or other robust native graminoids such as *Spartina alterniflora* or *Typha* L., might replace some of the biologically-controlled non-native *Phragmites*. However, at least in some situations, non-native *Phragmites* has been shown to exceed native *Phragmites* in rhizosphere oxygenation, photosynthetic rate, photosynthetic canopy, specific leaf area, nitrogen content, length of growing season, sexual reproduction, shoot density and height, biomass, and relative growth rate (Mozdzer and Zieman 2010; Kettenring and Mock 2012; Tulbure et al. 2012; Mozdzer et al. 2013), but it is not known how these traits might drive differences in ecosystem services overall. Also, as explained above, native *Phragmites* may be adversely affected by biocontrol of non-native *Phragmites.* The proposed biocontrol program may substantially reduce biomass and cover of native as well as non-native *Phragmites*. We disagree strongly with Blossey et al. (2018a), who “consider the potential threat to *P. australis americanus* demography by *A. geminipuncta* and *A. neurica* to be far smaller than allowing continued expansion of invasive *P. australis*.”

Conclusions

It is difficult to find host-specific biocontrol agents at the species level, and finding them at the subspecies level is especially challenging. *Phragmites australis* is not the only cryptic, subspecific invader; reed canary grass (*Phalaris arundinacea* L.) is another example (Nelson et al. 2014). We are concerned that Casagrande et al. (2018) and Blossey et al. (2018a) have downplayed our previously published analyses (Bhattarai et al. 2016; Cronin et al. 2016), namely that biocontrol insects targeting non-native *Phragmites* may cause substantial damage to native *Phragmites,* while not adequately addressing a well-established body of literature relevant to this question. Native *Phragmites* constitutes a unique and complex reservoir of genetic diversity and provides ecosystem services that could be lost with the introduction of a risky biocontrol agent. Previous responses by Blossey and Casagrande (2016a, b), and the recent publications by Casagrande et al. (2018) and Blossey et al. (2018a), have not satisfactorily addressed concerns surrounding the potential for damage to native *Phragmites.* Inasmuch as substantial reduction of native as well as non-native *Phragmites* across the North American continent could result from the proposed classical biological control, all of the relevant ecological, social, and economic concerns must be considered explicitly. Because both beneficial and detrimental effects of *Phragmites* are site-specific, and because biocontrol may harm native lineages as well as non-native *Phragmites*, management of *Phragmites* should be situational rather than general. We strongly disagree with the conclusions and recommendations of Casagrande et al. (2018) and Blossey et al. (2018a) and warn that approval of *Archanara* spp. as biocontrol agents for non-native *Phragmites* in North America could result in widespread ecological and socioeconomic impacts.

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Compliance with ethical standards

Conflict of interest The authors state they have no conflicts of interest.

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