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Grasses as appropriate targets in weed biocontrol: is the common reed, *Phragmites australis*, an anomaly?

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Abstract Despite their importance as invasive species, there has been a hesitation to target grasses in classical biocontrol. This historic bias appears to be changing with multiple active research and release programs. Similarly, biocontrol workers appear to avoid targeting species with native congeners. These biases appear inappropriate as the ecological and entomological literature provide abundant evidence for sub-genus specificity for many herbivores, including those attacking grasses. The biocontrol program targeting *Phragmites australis* (Cav.) Trin. ex Steud (Poaceae) provides an informative example with endemic subspecies in North America and many sub-genus specific herbivores, including potential European control agents. Grasses and target weeds with congeneric native species require rigorous host range testing, similar to all other targets in current weed biological control programs. Furthermore, it appears prudent to ask petition reviewers and regulatory agencies to abandon their focus on results of no-choice studies and to distinguish between trivial feeding and demographic impacts.

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Introduction

Two widely-held tenets of the current practice in weed biocontrol are: avoid targeting grasses and avoid plant pests with congeneric species (Pemberton 2000). Although there are 2176 species of invasive grasses worldwide, biological control of invasive grasses has historically been avoided because of the economic importance of many grass species and an expectation that a general lack of species-specific secondary chemistry among grasses would result in a lack of host specific herbivores and hence threaten safety of non-target species (Witt and McConnachie 2003). Pemberton (1996) summarized the status of grass biocontrol: "there has never been a biological control program against a grass weed and it is unlikely that one will be started against these plants in the future. The enormous value that grass family crops (like corn, wheat, rice, barley, sugarcane, etc.) have, and also the belief that natural enemies of grasses have less

specificity than those that feed on other plants have prejudiced this approach."

There are no good underlying ecological reasons why weed biocontrol scientists have failed to target grasses (Witt and McConnachie 2003). Grasses may be less structurally complex leading to a reduced diversity of feeding niches, and they may not offer the same array of secondary chemistry as many other herbaceous species, but they have their own highly specific insect (particularly Diptera and Hymenoptera) and pathogen communities (Witt and McConnachie 2003), some of which are major pests of crops, such as in rice or sugarcane (Lou et al. 2013; Settle et al. 1996; Strong et al. 1977; Zhu et al. 2000). Furthermore, grasses through mutualistic endophytes and silicone-based defenses (Djamin and Pathak 1967; Gali-Muhtasib et al. 1992; Hartley and DeGabriel 2016; Massey et al. 2007) have major impacts on vertebrate and invertebrate herbivores comparable to their broadleaf counterparts (Moore et al. 2014). The charge for biocontrol scientists is to assess whether host-specific species with potential to affect host plant demography are available among grass herbivores and pathogens.

Multiple Asian grasses are invasive in the USA and all of them have several species (mostly pathogens) that appear to have restricted host ranges (Zheng et al. 2004) providing opportunities to implement biocontrol. In 2000 the planthopper *Prokelisia marginata* (van Duzee) (Delphacidae) was introduced into Washington State in an effort to reduce populations of smooth cordgrass, *Spartina alterniflora* Loisel (Poaceae) (Grevstad et al. 2003). This was followed in 2009 and 2010 with releases of the gall wasp *Tetramesa romana* Walker (Eurytomidae) and the scale *Rhizaspidiotus donacis* Leonardi (Diaspididae) targeting giant reed, *Arundo donax* L. (Poaceae) (Racelis et al. 2009) with promising early results (Goolsby et al. 2016). Research is underway to assess feasibility of targeting cogongrass (*Imperata cylindrica* (L.) P. Beauv.) (Poaceae) and Japanese stiltgrass *Microstegium vimineum* (Trin.) A. Camus (Poaceae) (Nestory 2016; Overholt et al. 2016). The importance of grasses as invasive species and monetary expenditures currently dedicated to their control (Brooks et al. 2004; Martin and Blossey 2013b; Rossiter et al. 2003) clearly warrant a continued focus on evaluating potential for biocontrol. In this paper, we discuss opportunities to develop safe and effective classical

biological control programs when specificity of bio-control agents requires sub-generic levels of host specificity. In particular, we use ongoing research to develop biocontrol for introduced lineages of common reed, *Phragmites australis* (Cav.) Trin ex Steud (Poaceae) in North America, to illustrate these prospects.

Host specificity of herbivores at the sub-species level

Pemberton (2000) pointed out difficulties targeting introduced plants with native congeners, but noted that risks can be reliably evaluated. In fact, specificity of herbivores frequently occurs below species level (Fritz and Simms 1992) and in a recent review Whitham et al. (2012) show that genotype specificity is a widespread phenomenon listing examples from 29 genera within 15 plant families. The ecological and entomological literature on host plant resistance to insects is replete with examples of selectivity in response to genotypic variation in structural (Karley et al. 2016) or chemical defenses (Agrawal 2011; McGuire and Johnson 2006; Moore et al. 2014) and particularly including grasses. These variations in resistance have been known for a long time (Painter 1951) and allow resistance breeding in crops, for example in rice, where attack by 32 different insect herbivores is controlled by variation in resistance among strains and inter-specific rice hybrids (Heinrichs 1986). Other plant–herbivore systems expressing varietal resistance occur in wheat, oats, barley and maize, including attack of wheat by Hessian fly (*Mayetiola destructor* Say; Cecidomyiidae), or wheat stem sawfly (*Cephus cinctus* Norton; Cephidae) and many others (Painter 1951). Intra-specific variation in herbivore resistance is a common phenomenon and well-known for many crops in the Poaceae. Consequently, if we were looking for a genotype or subspecies-specific biocontrol agent, we would have several to choose from within these grasses. We acknowledge that resistance is not always complete or permanent and herbivores show gradients in attack among different genotypes (McGuire and Johnson 2006). The underlying reasons for this host or genotype specialization, previously assumed to be based on performance trade-offs, now appears to involve complex interactions of genetic architecture

and multitrophic interactions (Forister et al. 2012). But the evolutionary and ecological opportunity of sub-species level specificity is widespread and there is no a priori reason to reject grasses or species with close relatives as targets of biocontrol investigations due to beliefs that safety of non-targets is elusive in these systems.

The genus *Solanum* provides an interesting example with many important crops (potatoes, tomatoes, eggplant) and native species yet also problematic invasive species. In South Africa *Solanum eleagnifolium* Cav. and *S. mauritianum* Scopoli (Solanaceae) were targeted by releasing multiple agents including leaf beetles *Leptinotarsa texana* (Schaeffer) and *L. defecta* (Stål) (Chrysomelidae), a lace bug *Gargaphia decoris* Drake (Tingidae) and a flower bud weevil *Anthonomus santacruzi* Hustache (Curculionidae) (Hakizimana and Olckers 2013; Olckers 2000; Olckers and Hulley 1994). The herbivores established and recent evidence appears to suggest heavy and wide-spread impact on *S. eleagnifolium* (Winston et al. 2014). But with the exception of a single attack of eggplant at a single farm (Olckers, pers. comm. to Hariet Hinz) there are no reports of non-target feeding in the field (Olckers 2011), supporting decisions to release insects that show little feeding in host specificity tests on native relatives and crops. Despite important crop and native relatives, the pasture weed tropical soda apple, *Solanum viarum* Dinal (Solanaceae) is now under widespread control by the leaf beetle *Gratiana boliviana* Dunal (Chrysomelidae) in the USA (Diaz et al. 2014). Clearly, safety of non-target species is a function of host specificity of biocontrol agents and existence of closely related native species or important crops should not preclude investigations per se (Hinz et al. 2014).

We are only aware of two examples in weed biocontrol when sub-species level specificity was recorded. The first is rush skeletonweed (*Chondrilla juncea* L.) (Asteraceae) where existence of three different leaf morphotypes precluded success using the mite *Aceria chondrillae* Canestrini (Eriophyidae) and the rust fungus *Puccinia chondrillina* (Bubak & Syd.) (Uredinales). Both species show specificity at the morphotype level, limiting their ability to control all *Chondrilla* populations (Charudattan 2005; Winston et al. 2014; and references therein), although recent molecular work suggests a more complex and variable background of different genotypes, plant

morphology and insect attack (Gaskin et al. 2013). The second example is *Chrysanthemoides monilifera* ssp. *monilifera* (L.) T. Norl. (Boneset) and *C. monilifera* ssp. *rotundata* (DC.) T. Norl. (bitou bush) (Asteraceae). Both have sub-species specific biocontrol agents in Australia and New Zealand (Winston et al. 2014). Furthermore, genotypic diversity of *Lantana camara* L. (Verbenaceae) has been an obstacle to achieving more widespread biological control of the species (Crawley 1989) and there are additional examples of biotype or population variation in preference of weed biocontrol agents and their ability to control populations or biotypes (Winston et al. 2014) demonstrating prevalence of herbivore specificity or preference below the species level assigned by taxonomists.

Introduced *Phragmites* in North America

Impacts of introduced *P. australis* on native biota

Introduced *P. australis* genotypes in North America can dominate wetland plant communities and this invasive success has been linked to shoreline development in New England (Bertness et al. 2002; Burdick and Konisky 2003; Silliman and Bertness 2004), prevalence of agriculture and nutrient loading, (Kulmatiski et al. 2010; Sciance et al. 2016), salt tolerance (Vasquez et al. 2005), ability to exploit disturbances and dispersal corridors along roadsides (Brisson et al. 2010; Jodoin et al. 2008), and hydrology changes (Hudon et al. 2005). Wetland managers have responded with aggressive treatments due to concerns over detrimental impacts of *P. australis* on native North American biota (Hazelton et al. 2014; Marks et al. 1994; Martin and Blossey 2013b).

However, evidence for negative impacts on native biota is mixed and few long-term data exist to separate impacts of *P. australis* invasion from other stressors affecting wetlands such as land use history, changes in hydrology, nutrient loading, etc. (Kettenring et al. 2012). Introduced *P. australis* is thought to threaten endangered species such as the pallid sturgeon (*Scaphirhynchus albus*) (Acipenseridae), the whooping crane (*Grus americana*) (Gruidae), the northern Great Plains population of the piping plover (*Charadrius melodus*) (Ciconiiformes), and the interior least tern (*Sterna antillarum athalassos*) (Laridae) in the

Platte River (National Research Council 2004). Some, but not all, native wetland plants are negatively affected by *P. australis* encroachment (Crocker et al. 2017), as are some specialized marsh birds (Benoit and Askins 1999; Whyte et al. 2015) but not others (Parsons 2003). Similarly some turtles (Bolton and Brooks 2010), and small fish such as *Fundulus* spp. (Fundulidae) (Able and Hagan 2000) show population reductions in response to invasive *P. australis*. In contrast, several amphibians (Cohen et al. 2012, 2014; Martin and Blossey 2013a; Rogalski and Skelly 2012), some crustaceans (Able and Hagan 2000), Northern pike, *Esox esox* (Esocidae) (Larochelle et al. 2015), and decomposition processes and macroinvertebrate communities (Kennedy et al. 2012) appear to show no negative response to *P. australis* encroachment.

The anticipated negative ecological impacts, and reduced aesthetic and property values—particularly along the Atlantic Coast and the Great Lakes (Clawson and Duthinh 2015)—resulted in the designation of introduced *P. australis* as a noxious weed in Alabama, Vermont, Washington, Nebraska, British Columbia, and Alberta and the species is also listed as invasive or prohibited in Connecticut, Massachusetts, and South Carolina (USDA NRCS 2017). Introduced *P. australis* also has a long history of failed attempts to manage the species using chemical and physical means (Marks et al. 1994; Martin and Blossey 2013b). Only restoration of regular tidal inundation with full strength seawater can successfully suppress *P. australis* in coastal areas (Chambers et al. 1998). Short-term suppression of the species is possible using herbicides, while eradication is extremely difficult and only achievable for small populations not exceeding a few hundred square meters (Lombard et al. 2012; Quirion et al. 2018). Annual expenditures for herbicide use to treat *P. australis* in the USA alone reached US $4–5 million before 2010 (Martin and Blossey 2013b).

Development of biological control of invasive *P. australis*: research in North America

We initiated a classical biocontrol program in 1998. A literature review identified > 150 European herbivores, pathogens and inquilines with > 20 species listed as monophagous (Tewksbury et al. 2002). When detailed investigations began, the status of *P. australis* as native or introduced was contested, but now taxonomists recognize three distinct lineages, of

which at least one is endemic to North America (Saltonstall 2002, 2016; Saltonstall et al. 2004). This raises the necessity that any biocontrol agent for invasive *P. australis* requires sub-species level host specificity.

The most widespread and regionally abundant of three different *P. australis* lineages in North America are introduced European genotypes (Saltonstall 2002, 2016) which are widespread (Fig. 1b) from Canada to the Gulf Coast and southern California (Saltonstall and Meyerson 2016). An endemic North American sub-species *P. australis americanus* Saltonstall, P.M. Peterson & Soreng is genetically and morphologically diverse and occurs from Canada to northern Mexico (Colin and Eguiarte 2016; Saltonstall and Meyerson 2016) (Fig. 1a). The Gulf Coast lineage *P. australis berlandieri* (E. Fourn.) C.F. Reed occurs in the southern USA south through Mexico into South America (Fig. 1c) but the status of the lineage as native or introduced is unresolved (Colin and Eguiarte 2016; Lambertini et al. 2012; Saltonstall and Meyerson 2016). European genotypes are considered invasive with widespread detrimental impacts (Marks et al. 1994), while populations of native genotypes have been lost (Saltonstall 2002) and are considered of conservation concern in eastern states. Hybridization between European and North American lineages, long suspected due to common garden evidence (Meyerson et al. 2008) has been confirmed in New York and Nevada (Saltonstall et al. 2014, 2016). The range of the lineages overlap (Fig. 1) poses a constraint on the *Phragmites* biocontrol program. Potential biocontrol agents are required to be specific to invasive genotypes and not affect demography or reduce populations of endemic sub-species to be acceptable to regulatory agencies and wetland managers (Martin and Blossey 2013b).

There is abundant evidence of strong sub-species level selectivity in the field among three native North American *Phragmites* herbivores and 18 European species already accidentally introduced to North America (Blossey 2003a; Blossey and Casagrande 2016). Three native *Phragmites* specialists (*Calamomyia phragmites* Felt, Cecidomyiidae; *Thrypticus willestoni* (Wheeler), Dolichopodidae; and *Ochlodes yuma* (Edwards), Hesperiidae) all occur exclusively on native *P. australis americanus* and have never been recorded on introduced or Gulf Coast genotypes. Ten of 18 accidentally introduced *Phragmites* herbivores
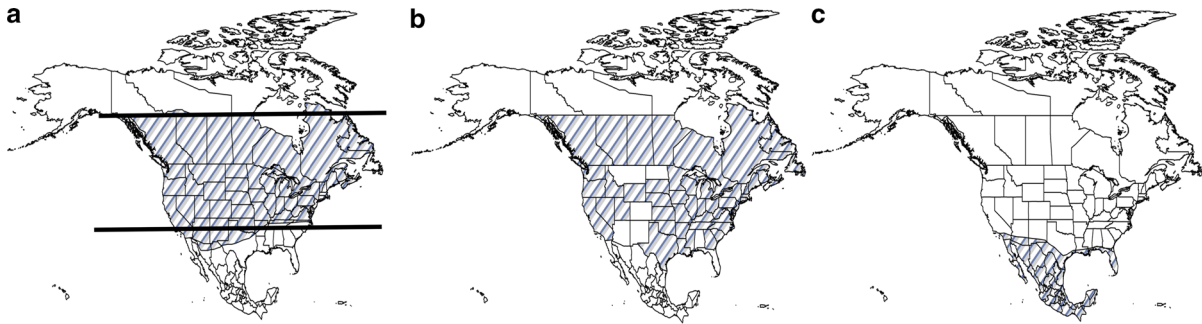
Fig. 1 Distribution (hatched areas) of **a** native *P. australis americanus*, **b** introduced *P. australis australis*, and **c** *P. australis berlandieri* in North America. Maps drawn and updated based on Saltonstall and Meyerson (2016), USDA PLANTS database (https://plants.usda.gov), and our own records using fied surveys and submitted samples. Please note that occurrences at range margins and areas where introduced *P. australis* is currently advancing have great uncertainty due to sampling limitations. Expected northern and southern distribution of *A. geminipuncta* and *A. neurica* are indicated by parallel lines across North America in (**a**) and are based on climate conditions in their native European ranges (https://upload.wikimedia.org/wikipedia/commons/9/92/Annual_Average_Temperature_Map.png)

are specialists on *Phragmites* and the others are polyphagous. Among these specialists *Lasioptera hungarica* Möhn (Cecidomyiidae), *Giraudiella inclusa* (Frauenfeld) (Cecidomyiidae), *Lipara pullitarsus* Doskocil & Chvála (Chloropidae) and *Rhizedra lutosa* (Hübner) (Noctuidae) are only recorded feeding on introduced *P. australis*, although *L. hungarica* also attacks hybrids in New York (Saltonstall et al. 2014). Thus seven of 13 *Phragmites* specialists presently known to be in North America show specificity at the sub-species level as currently defined by taxonomists and the remaining six species are found on both native and introduced *P. australis*.

Specialist herbivores of *Phragmites* in Europe

Nine European insect herbivores were chosen for further investigations as potential biocontrol agents based on their feeding niche, damage inflicted, and reported host specificity (Tewksbury et al. 2002). This list was narrowed to the four most promising agents (Häfliger et al. 2005, 2006a, b) and for two species of noctuid moths, *Archanara geminipuncta* (Haworth) and *A. neurica* (Hübner) (Noctuidae). Extensive host specificity testing is now complete (Blossey et al. 2018). We focus on these two stem mining univoltine noctuids because they are the most widespread, abundant, and with the largest additive impact on *P. australis* (Häfliger et al. 2006b).

Detailed life histories are well known with adults flying in July/August and eggs laid under leaf-sheaths where they overwinter until larvae hatch in early spring (Häfliger et al. 2006b). Larvae feed internally in shoot tips and upper internodes and need to change stems multiple times before pupating in lower sections of *P. australis* stems. In Europe, large population fluctuations are reported with outbreak cycles of 3–4 years when stem damage may reach 100% (Michel and Tscharntke 1993; Tscharntke 1990). Shoot heights and above-ground biomass reductions can be substantial, typically 20–60% (Häfliger et al. 2006a) but occasionally reaching 100% and intensity of damage may be a function of latitude (Tscharntke 1990, 1992b, 1999). Due to extensive shoot damage in Europe, *A. geminipuncta* is considered a keystone species influencing trophic structure and abundance of reed biota from insects to birds (Tscharntke 1989, 1992a, 1999).

Our host specificity testing followed established guidelines and was conducted in quarantine at the University of Rhode Island as well as in the native range at CABI in Switzerland (Blossey et al. 2018) with a particular focus on ability of neonate larvae to penetrate or survive in stems of other plant species. Larvae of *A. geminipuncta* and *A. neurica* were unable to survive in any of the 43 non-target test plant species, but both were able to complete development in invasive *P. australis* and native *P. australis americanus* (under no-choice conditions). We followed up with oviposition choice experiments on potted plants

at CABI from 2011 to 2015, allowing mated females to choose among different European, invasive North American, and endemic North American genotypes that were offered in monospecific and mixed arrangements. Under these experimental conditions *A. neurica* laid 6.7% (39 of 584) and *A. geminipuncta* laid 6.5% (32 of 503) of their eggs on *P. australis americanus* with the remainder nearly evenly split among ancestral European and invasive North American *P. australis* (Blossey 2014; Blossey et al. 2013, 2018).

An overview of factors mitigating potential risks

Both *A. neurica* and *A. geminipuncta* lay few eggs on the endemic native sub-species *P. australis americanus* and their larvae are able to penetrate stems and develop successfully. We consider demographic risks for *P. australis americanus* to be low for the following reasons:

Leaf-sheaths

One important trait shared by native *P. australis americanus* across the range of the lineage are loose leaf-sheaths that fall off during fall and winter, while leaf-sheaths on invasive *P. australis* are retained, often for multiple years after senescence (Blossey 2003b; Ward 2010). What potential ecological benefits are derived from loose leaf-sheaths in North America is unknown, but it obviously deters oviposition by insects, such as *A. geminipuncta* and *A. neurica*. Females avoid loose leaf-sheaths, a behavioral trait which largely restricts attack to introduced *P. australis* (Blossey et al. 2013). Eggs attached to leaf-sheaths that fall off the plant show reduced survival rates (Blossey et al. 2018), hence choosing tight fitting leaf-sheaths for oviposition confers fitness advantages.

Larval shoot change

All *Archanara* larvae need to change shoots to complete development. The endemic *P. australis americanus* generally, but not always, occurs in small isolated populations with greatly reduced stem densities intermixed with many other wetland species. The probability for foraging larvae to successfully locate new stems is likely to be greatly reduced as stem densities decrease (Crawley and Gillman 1989), although no quantitative data on larval dispersal behavior are currently available for our system.

Demography

The goal of invasive *P. australis* management is to reduce negative impacts on native biota and ecosystem processes. To reach this goal it is generally assumed that management needs to greatly decrease abundance of the invasive lineage. Substantial stem mortality and reduction in rhizome growth is required to affect performance (Häfliger et al. 2006a) and subsequently demography in a species that is able to spread by seed and via rhizome growth. The low numbers of eggs laid on native stems is unlikely to result in substantial stem mortality or a demographic threat (Häfliger et al. 2006a; Myers and Sarfraz 2017).

Rapid evolution is unlikely to overcome resistance traits in *P. australis americanus*

We acknowledge the possibility that over evolutionary time different preferences may evolve, but the experimentally determined fundamental host range has been stable for weed biocontrol agents (Marohasy 1996; Suckling and Sforza 2014; van Klinken and Edwards 2002) even when species were re-tested decades after their introduction (Arnett and Louda 2002). Introduction of ecological novelty, for example by introduced plants, provides ample opportunity for herbivores to expand their realized host range as expressed in the field (Jahner et al. 2011) and this is often interpreted as a host shift or rapid evolution of host specificity (Secord and Kareiva 1996). But, in most cases, model organisms used to assess such host shifts, or changes in preferences based on feeding experience of larvae or adults are oligo- or polyphagous species (Anderson et al. 2013; Austel et al. 2014; Carrasco et al. 2015; Liu et al. 2005; Profitt et al. 2015). Their diet specialization is quite different from biocontrol agents that are typically monophagous in the field, and where we experimentally determine their fundamental host range.

Diets of insect herbivores change over time and both generalists and specialists may acquire new hosts (Futuyma and Agrawal 2009), and this acquisition may best be evaluated using a phylogenetically informed trait-based approach (Barrett and Heil

2012; Pearse et al. 2013; Pearse and Hipp 2009). The vast majority of phytophagous insects show "phylogenetic conservatism" retaining their association with plant taxa over millions of years (Futuyma and Agrawal 2009). Biocontrol agents passing through host range testing, as far as we can tell from decades of observation and study, appear particularly "conservative" (Blossey et al. 2001; Hinz et al. 2018; Suckling and Sforza 2014).

In the particular case of *P. australis americanus* we consider that this lineage is particularly safe from potential rapid evolutionary adaptations of the herbivores should introduction of *A. geminipuncta* and *A. neurica* be granted because the response to loose leaf-sheaths is behavioral, not physiological. This plant-specific trait actually adds to the safety of native genotypes. Evidence from host shifts of herbivores suggests that adaptations to process plants with different defense chemistry, or changes in female recognition of host plants that allow successful larval development are relatively "easy routes" to incorporate novel hosts (Pearse et al. 2013). However, recognition and palatability are only two of the many traits that determine the ability of herbivores to utilize plants (Barrett and Heil 2012). Larvae of both *Archanara* species can be reared in native *P. australis americanus* stems. This lineage is clearly part of the physiological host range and there appear to be few performance penalties (Blossey et al. 2018). However, as detailed above, loose leaf-sheaths can be considered a resistance trait preventing oviposition by *Archanara* species. This plant trait of *P. australis americanus* is not affected by selection operating at the herbivore level, therefore there is no pathway for rapid selection or evolutionary change operating at the level of the insects to favor genotypes that would oviposit under loose leaf-sheaths while maintaining herbivore fitness.

Ability for local management

While we believe that limited stem damage by the two *Archanara* species on endemic genotypes would not amount to a demographic threat, the fact that eggs overwinter under leaf-sheaths that adhere to shoots (or drop to the ground) affords a potential ability to manage a local population using controlled burns should it be necessary (Branson et al. 2015; Brix et al. 2014; Vogel et al. 2010). Land managers could burn or

mow/mulch the stand, thereby locally managing the noctuid populations.

Distribution and climate

The Gulf Coast subspecies grown in pots in our common garden in Switzerland developed only extremely thin side stems. We therefore lack reliable oviposition preference data that we have for *P. australis americanus*. However, the European distributions of *A. geminipuncta* and *A. neurica* (Fig. 2) offer some limited evidence that these species may not be able to thrive as far south as *P. australis berlandieri*, a sub-species restricted to areas where average annual temperatures range from 17 to 21 °C. In Europe, neither moth is found where average temperatures exceed 15 °C and based solely on climate data, we expect the herbivores, if released, to establish in temperate North America (Fig. 1a). However, prediction of future ranges based on ancestral distributions is notoriously unreliable (Shabani et al. 2016) and species respond, including evolutionarily (Bean et al. 2012) to more than climate. Thus caution is appropriate in anticipating future distributions. Only detailed studies after release will be able to assess how well home-range climate data may predict novel range distributions.

Regulatory considerations

Our case study on *P. australis* shows that sub-species level specificity may be more common than is often assumed, including for species in the Poaceae. But special scrutiny is certainly required, including evaluation and proper weighting of evidence collected in different venues and with different methodologies. Within the US regulatory framework, there has been a tendency to regulate based upon no-choice test results, ignoring important factors determining fundamental and ecological host ranges or demographic impacts, which in science guided decision making should override data on trivial and inconsequential cosmetic feeding (Blossey 2016a, b; Cristofaro et al. 2013; Hinz et al. 2014; Smith 2012). Our results, and those of others, have demonstrated the existence of sub-species level selectivity in herbivorous insects, extending opportunities for weed biological control. The past history of bias or hesitation to assess weed biocontrol
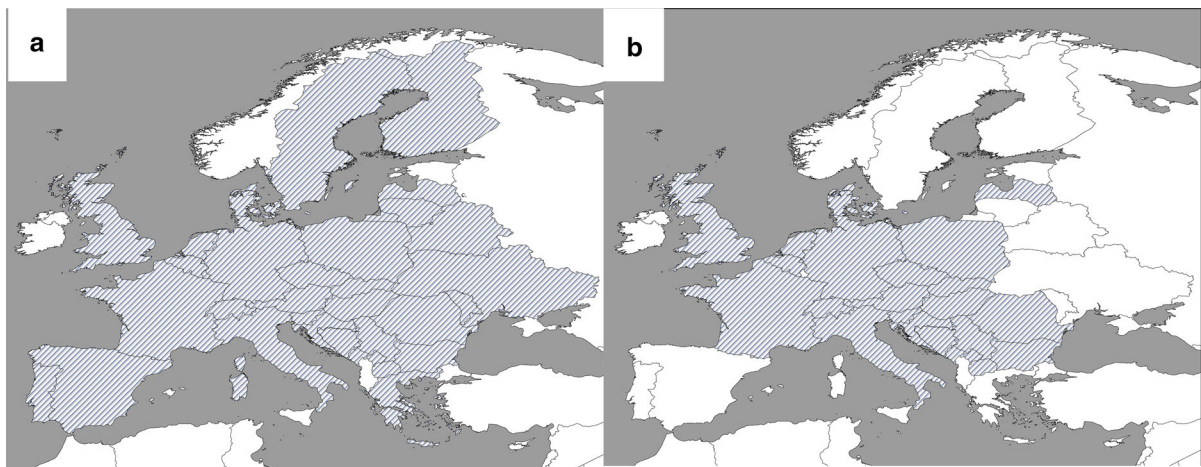
Fig. 2 Distribution (hatched areas) of *Archanara geminipuncta* (**a**) and *A. neurica* (**b**) in western, central and eastern Europe. Please note that occurrences at range margins have great uncertainty due to sampling limitations. *Source*: http://www.fauna-eu.org

potential based on problematic assumptions about close relatives or grasses was not based on sound understanding of ecological or evolutionary relationships.

Recent revisions to guidance documents (USDA 2016) indicate that minor probing, as *Archanara* larvae do on some non-target species, is considered "non-feeding". The document further states that "arthropods may ingest enough material on certain plants to produce droppings. However, if the life span of the organism will be extended but there is little evidence of continued development, then these accepted but unsuitable species can also be discarded as potential host plants" (USDA 2016). Laboratory testing and abundant evidence from the field assures that neither of our selected species feeds and develops on any crop plant (or any species outside the genus *Phragmites*), further satisfying USDA/APHIS requirements that introduced species are not potential plant pests of species of economic importance, as required under the Plant Protection Act.

Furthermore, the National Environmental Protection Act requires that releases do not present a risk to the environment and the US Fish and Wildlife Service (USFWS) reviews petitions to ensure that potential biocontrol agents do not pose any risk to threatened or endangered species. While we have documented the potential for *A. geminipuncta* and *A. neurica* to occasionally oviposit (< 7% of all eggs) on endemic *P. australis americanus*, we believe that the potential demographic consequences are minimal, especially

compared to threats the species faces from invasive *P. australis* encroachment (Saltonstall 2002). Furthermore, native endemic *P. australis americanus* is not a listed species, and while we need to safeguard any species, this will in essence reduce USFWS review to species that may be indirectly affected via food web connections or changes in wetland structure (Lampert et al. 2014). Both *Archanara* species are important food sources for a number of European birds as well as insect parasitoids and predators (Tscharntke 1992a, b), and *P. australis* is not known to possess any potentially toxic secondary chemistry. Therefore, there should be no concerns about potential harm to predators of *Archanara* larvae or adults, whether they be birds, bats, or other vertebrates or invertebrates.

Considering potential threats to other wetland biota, we are left with concerns regarding the potential of rapid death of extensive *P. australis* monocultures. This was a concern that halted herbicide management of *Spartina* in California to spare habitat of the endangered California rail (Lampert et al. 2014). Similar concerns over rapid defoliation of *Tamarix* spp. (Tamaricaceae) by the biocontrol agent *Diorhabda carinulata* Desbrochers (Chrysomelidae) affecting breeding habitat of the endangered southwestern willow flycatcher *Empidonax traillii extimus* (Tyrannidae) led to a withdrawal of release permits (Dudley and Bean 2012). Based on European evidence, we recognize the potential for outbreaking *Archanara* populations. However, unlike herbicide or mechanical treatments (both often followed by spring

burns), with biocontrol, at least in this case, dead standing biomass will remain in place. This provides shelter and cover for wetland biota such as marsh birds or invertebrates foraging in flooded or moist soils. While there may be increased light penetration following years of noctuid outbreaks, this is desired to allow native wetland plant recruitment.

Conclusions

Invasive *P. australis* is one of the most widespread and successful invasive species in North America (Chambers et al. 1999; Kettenring et al. 2012; Saltonstall and Meyerson 2016) with a long history of failed management using physical and largely chemical means at enormous expense and with a dearth of information about impacts of management of wetland biota (Hazelton et al. 2014; Marks et al. 1994; Martin and Blossey 2013b; Quirion et al. 2018). Allowing continued expansion of the invasive lineage would not only jeopardize native wetland biota but also threaten the existence of endemic *P. australis americanus* (Saltonstall 2002). While we cannot be certain about the contribution of *A. geminipuncta* and *A. neurica* to potential reductions in invasive *P. australis* performance or demography, we consider risks of releasing these two species to *P. australis americanus* very small compared to effects of further unabated invasive *P. australis* encroachment or even continued unselective management using herbicide.

Although grasses such as *P. australis* and target weeds with many congeneric native species require rigorous host range testing, evolution has provided biocontrol scientists with an enormous diversity of herbivores—no different from other targets in current weed biological control programs. The host plant resistance literature, not often discussed among biological control researchers, provides many examples of extreme (genotype, chemotype or morphotype-based) host specificity among insect herbivores of many crops, including many grasses. Among the insect herbivores of *P. australis* known in North America, host specificity at the sub-species level is common in the field. Based upon extreme ovipositional preference, plant characteristics, and their European distribution, we expect that the two *Archanara* species under consideration for release in North America will demonstrate field-level host specificity,

limiting their reproduction and restricting their impact to introduced *P. australis*. The native lineages are safeguarded by a number of different morphological features, particularly lack of adherence of leaf-sheaths. Successful classical biological control of the invasive sub-species of *P. australis* in North America would provide incentive for addressing other challenging targets in classical biological control of weeds. We argue that each weed biocontrol agent should be evaluated on its own merits and reviews should be based on clearly articulated and reliable host specificity criteria, not whether the host plant belongs to a taxonomic group (like the Poaceae) or on the existence of many close relatives. As Pemberton (2000) states, erroneous beliefs and prejudice have prevented targeting grasses with biological control. Many of these species may offer appropriate targets without jeopardizing safety of native species or ecosystems.

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Bernd Blossey develops weed biocontrol programs and he assesses evolution of introduced species and impacts of multiple stressors, including invasive plants, earthworms and deer on wetland and forest food webs.