Evolutionary Applications www.evolutionaryapplications.org

Evolutionary Applications ISSN 1752-4571

PERSPECTIVE

Underutilized resources for studying the evolution of invasive species during their introduction, establishment, and lag phases

Travis D. Marsico,[1] Jennifer W. Burt,[2] Erin K. Espeland,[3] George W. Gilchrist,[4] Mary A. Jamieson,[5] Leena Lindström,[6] George K. Roderick,[7] Sarah Swope,[8] Marianna Szűcs[9] and Neil D. Tsutsui[7]

1 Department of Biological Sciences, Mississippi State University, Mississippi State, MS, USA
2 Department of Plant Sciences, University of California-Davis, Davis, CA, USA
3 Northern Plains Agricultural Research Lab, USDA ARS, Sidney, MT, USA
4 Department of Biology, College of William and Mary, Williamsburg, VA, USA
5 Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA
6 Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland
7 Department of Environmental Science, Policy and Management, University of California-Berkeley, Berkeley, CA, USA
8 USDA Exotic and Invasive Weeds Research Unit, Albany, CA, USA; and Department of Ecology and Evolutionary Biology, University of California-Santa Cruz, Santa Cruz, CA, USA
9 Plant, Soil, and Entomological Sciences, University of Idaho, Moscow, ID, USA

Keywords
biological control, evolution, horticultural invasion, invasive species, lag phase, natural history collections, specimens.

Correspondence
Travis D. Marsico, Present address: Department of Biological Sciences, Arkansas State University, PO Box 599, AR 72467, USA.
Tel.: 870-972-3082;
fax: 870-972-2638;
e-mail: tmarsico@astate.edu

Received: 9 September 2009
Accepted: 17 September 2009

doi:10.1111/j.1752-4571.2009.00101.x

Abstract

The early phases of biological invasions are poorly understood. In particular, during the introduction, establishment, and possible lag phases, it is unclear to what extent evolution must take place for an introduced species to transition from established to expanding. In this study, we highlight three disparate data sources that can provide insights into evolutionary processes associated with invasion success: biological control organisms, horticultural introductions, and natural history collections. All three data sources potentially provide introduction dates, information about source populations, and genetic and morphological samples at different time points along the invasion trajectory that can be used to investigate preadaptation and evolution during the invasion process, including immediately after introduction and before invasive expansion. For all three data sources, we explore where the data are held, their quality, and their accessibility. We argue that these sources could find widespread use with a few additional pieces of data, such as voucher specimens collected at certain critical time points during biocontrol agent quarantine, rearing, and release and also for horticultural imports, neither of which are currently done consistently. In addition, public access to collected information must become available on centralized databases to increase its utility in ecological and evolutionary research.

Three phases necessary for a successful biological invasion are introduction, establishment, and expansion or spread (Sakai et al. 2001). Successful transport to the novel habitat is a precursor to an introduction and is sometimes included as the first phase of invasion. The datasets we discuss in this perspective rely on successful transport; therefore, transport is not a focus of this article. Instead, we focus on how information gleaned from three underutilized data resources is useful for understanding species invasions beginning at the introduction phase. Introduction can be defined as the escape, release, dissemination, or placement of a species into a novel location or environment as a result of human activity (Executive Presidential Order 1999). After introduction, a successful invasive species becomes established in its new location, wherein it must initiate and maintain viable, self-sustaining populations (Sakai et al. 2001). Often an established exotic species remains at low population levels for a period of time during what is typically referred to as a lag phase (Kowarik 1995). After establishment and possibly a lag phase, an invasive species disperses and expands its geographic range and increases in population sizes to the point of causing economic harm or ecological damage (Executive Presidential Order 1999; Sakai et al. 2001).

To become a widespread and damaging invader, introduced propagules must successfully negotiate each stage, but the mechanisms involved in these transitions are difficult to study and often remain unclear. Because most invasive species are identified during their expansion phase and because the genetic identity of founding populations is often unknown (but see Grapputo et al. 2005; Dlugosch and Parker 2008b), it has been difficult to tease out the relative contributions of introduction history, population bottlenecks, lineage sorting, and *de novo* mutations to invasion success. Data collection on the early phases of invasion is generally retrospective and therefore limited. In this study, we highlight three sources of data that may be useful in understanding the processes that operate in the particularly poorly characterized early stages of invasion: introduction, establishment, and lag phases. Understanding these early phases of biological invasions is necessary to understand the factors involved in species colonizations and to better predict and reduce the negative impact of invasive species. We discuss the data available on biological control organisms, horticultural introductions, and natural history collections, and how these data can be used to understand intersections between ecological and evolutionary processes in the early phases of biological invasions.

Not all introduced species become invasive; yet the failure of introductions is poorly understood. It has been hypothesized that of the species introduced into novel habitats, 10% or less become established and of those, approximately 10% become invasive (Williamson and Fitter 1996), though the actual success rate may depend on the taxonomic group (Forsyth and Duncan 2001; Jeschke and Strayer 2005; Suarez et al. 2005). Failure to persist beyond the establishment and lag phases has been explained as the result of ecological factors such as inappropriate climate, intense competition, unsuitable disturbance regime, predation, or disease (Sakai et al. 2001). In addition, stochastic processes (Mack and Erneberg 2002) or failure to reach a spatial (Schoener and Schoener 1983) or numerical (Richter-Dyn and Goel 1972) critical patch size have been implicated in invasion failure. An expansion may be incited by an environmental change, such as a shift in abundance of a mutualist species or a change in disturbance frequency (summarized in Keitt et al. 2001). Adaptive evolution to conditions in the non-native range may be critically important in the transition to the expansion phase of invasions (Sexton et al. 2002; Yoshida et al. 2007; Suarez and Tsutsui 2008; Whitney and Gabler 2008). Evolutionary considerations such as effective population size (Phillips et al. 2008) and maladaptation (Hufbauer 2002; Memmott et al. 2005) have been shown to play a role in the ability of an introduced species to reach the expansion phase. In some cases, however, expansion may ultimately depend on the intrinsic biology of the invading species and may not be influenced by evolutionary forces during the early phases of invasion (Crawley 1986; Radosevich et al. 2003). For example, woody tree species with a long generation time simply may require time to reach reproductive maturity before expansion can occur (Wangen and Webster 2006).

For some species that become invasive, the rate of spread after introduction is constant, and the species expand directly after being introduced (e.g. Crowell 1973; Ebenhard 1987). Often, however, the rate of spread is slowed after establishment, and a lag in population growth is experienced prior to range expansion (Pyšek and Prach 1993; Hobbs and Humphries 1995; Hastings 1996; Frappier et al. 2003; Wangen and Webster 2006). The slow population growth rates that define the lag phase appear to vary among species and may be either positive or negative. Lag times with low but non-negative growth rates can be explained by purely spatial dynamics (Hastings 1996) or stochasticity (Lande 1998). Even without taking into account ecological factors, lag times can also be explained by simple logistic population growth (Sakai et al. 2001). The lag phase of invasions is often attributed to negative density dependence (e.g., Allee effects), as negative population growth rates are often observed when a species is at low densities (Getz 1996; Tobin et al. 2007). While Allee effects are commonly cited as an explanation for the lag phase, lag times can occur as a result of neutral processes. Long periods between reproductive events (Wangen and Webster 2006), spatial heterogeneity (Hastings 1996), and variable connectivity (Floerl et al. 2009) all can contribute to the ending of the lag phase and the start of the expansion phase. Furthermore, introduced species may experience evolutionary consequences of small population sizes that contribute to the lag phase (Suarez and Tsutsui 2008). Upon introduction, invading species often have low genetic diversity and may be more susceptible to genetic drift. Nevertheless, adaptive evolution has been documented to occur even after genetic bottlenecks (reviewed in Dlugosch and Parker 2008a), and such evolution may be critical for overcoming the consequences of Allee effects (Kanarek and Webb 2010). Studies that investigate ecological and evolutionary processes during the early phases of invasion are difficult because they often require retrospective datasets (but see Memmott et al. 2005; Fauvergue and Hopper 2009), yet these studies are critical for understanding biological invasions (Yoshida et al. 2007).

Biological control organisms, horticultural introductions, and natural history specimens are tractable datasets for evaluating the importance of evolutionary processes on successful introduction and establishment before invasive expansion (Table 1). These sources of data provide information on species introductions that may or may not result in successful establishment. Moreover, for established species, data are useful for both invasive and noninvasive species. All three sources of data potentially provide demographic, phenotypic, and genotypic data at multiple time points during the invasion process, including immediately after introduction and before invasive expansion (Table 2). Although correlative data alone are insufficient to establish causality, these data form a critical foundation of knowledge that can be used to guide and inform future manipulative experiments. As such, these three sets of data offer an opportunity to formulate and investigate hypotheses related to ecological and evolutionary factors that may facilitate understanding of the early stages of species invasions.

Ecological niche modeling also is an important research tool that can be used to predict the non-native range of invasive species, but because it does not inform the evolutionary processes involved in the early stages of invasion, we do not cover it in detail here (but see Peterson 2003;

Table 1. Summary of research questions in ecology and evolution of early-stage invasions that can be addressed with data from biocontrol releases (BIOC), horticultural introductions (HORT), and natural history collections (COLL). Studies using these datasets often will provide correlative evidence for ecological conditions necessary for establishment or the role of evolution early in the invasion process. Manipulative experiments based upon correlative findings then can be used to test specific hypotheses.

Research question	Data needed	BIOC	HORT	COLL
What are the characteristics of a location/ecosystem/community that	Ecology of the introduction location	Yes	Current only*	Limited
may facilitate establishment?	Establishment success/failure	Yes	Yes	Success only
What intrinsic (pre-introduction) biological aspects of a species might predispose it to becoming an invader?	Traits (genetic and phenotypic) exhibited in source population(s) correlated with establishment success/failure in introduced range	Yes	Yes	Sometimes
	Traits exhibited in introduced range correlated with invasion success/failure	Yes	Yes	Yes
What is the role of propagule pressure, effective population size, and founder effects on invasion?				
Is the population size of introduction correlated with invasion success?	The population size (*N*) at introduction	Yes	Ordinal only	No
Is the number of introductions at a single location correlated with invasion success?	Introduction/importation dates and source populations	Yes	Yes	Sometimes
Are introductions at multiple locations correlated with invasion success?	Source population and introduction locations	Yes	Yes	Sometimes
How important is evolution (selection, genetic drift, gene flow, and mutation) in the establishment and lag phases of invasion?	Genetic change over time (functional and neutral genetic markers can be used to answer different questions regarding specific microevolutionary processes)	Yes	Yes†	Yes
How important are preadaptation, the mixing of historically allopatric	Genetic identity of founding individuals (voucher specimens) -or-	Yes	Yes	Yes
populations, and founder effects on establishment?	Manipulate population genetics, source populations, and/or phenotypic traits prior to introduction, then track establishment	Yes	Inadvisable‡	No

*The ecology of the location at the date of introduction is unlikely to be recorded.

†Cultivated individuals can be compared with established wildland individuals, providing information at two time-points along the invasion pathway.

‡ However, *post hoc* comparisons of different nursery practices (clonal propagation versus selective breeding) can be conducted.

Table 2. Summary of biocontrol, horticultural trade, and natural history collection databases for investigations of ecology and evolution in early-stage invasions. This summary does not include meta-analyses or single-species data, but it does include potentially available data from each source, given the appropriate level of support.

Dataset	Introduction data	Climatic and/or geographic area of origin	Establishment success	Establishment failure	Vouchers/genetic identity	Ecological data	Available online?
Biocontrol							
APHIS	Date, location	Yes	No	No	No	No	No
ROBO*	Date, *N*, location	Yes	No	No	Yes	No	Yes
BLM	Date, location	Unknown	Yes	No	No	No	No
BIRLDATA	Date, *N*, location	Yes	Unknown	Unknown	Yes	No	No
EPPO	Date	Yes	Yes	Yes	No	No	No
BCDC	Date, *N*, location	Yes	Yes	Yes	No	Yes	Some
Potentially available	*Date, N, location*	*Yes*	*Yes*	*Yes*	*Yes*	*Yes*	*Yes*
Horticultural introductions							
APHIS-PIN	Date (for some species)	No	No	Yes†	No	No	No
Potentially available	*Date, location*	*Yes*	*Yes*	*Yes*	*Yes*	*Yes*	*Yes*
Natural history collections							
Invaders database‡	Possibly date and location, linked§	General	Yes	No	Yes, linked	Limited	Yes
PLANTS database¶	Sometimes	General, linked	Yes	No	Yes, linked	Limited	Yes
NBII**	Possibly date and location, linked	Sometimes, linked	Yes	Rarely††	Yes, linked	Yes, linked	Yes
GBIF‡‡	Possibly date and location, linked	Sometimes, linked	Yes	No	Yes, linked	Yes, linked	Yes
Lifemapper§§	Possibly date and location, linked	Sometimes, linked	Yes	No	Yes, linked	Yes, linked	Yes
OBIS¶¶	Possibly date and location, linked	Sometimes, linked	Yes	No	Yes, linked	Yes, linked	Yes
Potentially available	*Date, location*	*General*	*Yes*	*Rarely††*	*Yes*	*Yes*	*Yes*

*http://www.ars-grin.gov/nigrp/robo.html.
†All horticultural species not established in wildlands may be considered 'establishment failures'.
‡http://invader.dbs.umt.edu.
§'Linked' indicates that data available on databases/portals are compilations of collection information from more than one physical location.
¶http://plants.usda.gov.
**http://www.nbii.gov.
††Port-of-entry samples, for example, can be used to identify introduced species that fail to become established.
‡‡http://www.gbif.org.
§§http://www.lifemapper.org.
¶¶http://www.iobis.org.

Graham et al. 2004; Wiens and Graham 2005). Nevertheless, ecological niche models are an important complement to the ideas we propose here for increasing the use of each of these datasets, and ecological models should be used to predict the potential range of successfully spreading biocontrol and horticultural species. Results from these models then can be used to hone investigative strategies into evolutionary processes in specific invasive taxa; for example, invasive species that have expanded beyond their predicted non-native range may be selected for study as species that potentially evolved in their non-native range. Similarly, species that match their predicted range may be explored in detail as species that potentially invaded successfully with little evolution.

Use of biological control organisms for the study of early phases of invasion

The linkage between invasion biology and biological control has long been recognized (Wilson 1965), and biological control practice has the potential to serve as a testing ground for several ecological and evolutionary theories regarding species invasions (Kareiva 1996; Ehler 1998; Fagan et al. 2002). As introduction of a biocontrol agent is deliberate, biocontrol provides one of the few opportunities to observe the dynamics that occur during the initial phases of invasion. Biocontrol releases can be viewed as ecological and evolutionary experiments testing successful establishment in different habitats, with different biocontrol agent populations, and with different propagule pressure. Thus, more emphasis can be placed on the evolutionary processes at the early stages of invasion, given there is an appropriate focus on individual- and genetic-level recordkeeping during the releases. Some researchers in certain systems are already making use of these advantages. For example, the ladybird *Harmonia axyridis* was introduced as a biological control agent to Europe and North America. In Europe, it is now considered an invasive species and is being used to study invasion mechanisms (Adriaens et al. 2008; Brown et al. 2008; Lombaert et al. 2008). Brown et al. (2008) studied the early stages of invasion by tracking the distribution changes of the ladybird from the first year of its arrival in Great Britain, and Lombaert et al. (2008) compared laboratory biocontrol versus invasive populations of *H. axyridis* to assess differences in adaptive phenotypic plasticity, which they found for some of the metrics measured. These studies indicate that biological control may contain fruitful and untapped information resources that can address the role of evolution in the establishment and spread of invasive populations.

In addition to establishment and expansion successes, the failure of a biocontrol agent may provide insights into the factors that distinguish successful invaders from those that are unable to become established. Biocontrol organisms have been chosen for certain criteria, both their own and of their hosts (McFadyen 1998), which may affect the likelihood of establishment and spread. Often these criteria have not been consistent (McFadyen 2000); however, the criterion of host specificity is fundamental to regulation and safety and thus biocontrol agents represent only this subset of possible invaders.

When multiple, geographically separated, native-range source populations are used as collection sites for potential biocontrol agents, the opportunity exists for investigating functional genetic differences among the sources. These genetic differences may influence establishment success depending upon preadaptation to the release sites (McDonald 1976). In addition, large-scale laboratory rearing may incite evolution in laboratory conditions that has the potential to influence success when the biocontrol agents are released in the field (Bush and Neck 1976; Lombaert et al. 2008). Genetic diversity and genetic change in the laboratory have the potential to answer questions about necessary preadaptation and the effects of uniting historically allopatric populations in the field once releases begin (Hopper et al. 1993).

Because biocontrol organisms are susceptible to potential Allee effects (Fauvergue and Hopper 2009), they may make particularly good models for the study of how different types of Allee effects may constrain or even promote evolution in invasions. Lack of persistence of small populations due to Allee effects may actually buffer the entire species from drift processes (Kramer and Sarnelle 2008), while persistent small populations are vulnerable to genetic drift. The outcome of the interaction between demographic and evolutionary effects may be influenced by the component Allee effect that is exhibited. For example, Allee effects due to initial overdispersal (Jonsen et al. 2007) may have different outcomes than reproduction that is dependent on sociality (Hee et al. 2000). While biocontrol organisms present the potential to study a wide range of Allee effects, they also provide the opportunity to study invasions free from Allee effects altogether, as parasitoid wasps, a large group of biocontrol organisms, are unlikely to experience any density-dependent dynamics at low densities (Fauvergue et al. 2007; but see Fauvergue and Hopper 2009). There is a paucity of work addressing the evolution of biocontrol organisms in their introduced range (Roderick and Navajas 2003; Hufbauer and Roderick 2005), but there is emerging evidence that evolution is associated with establishment (Phillips et al. 2008; but see Hufbauer 2001). We argue that data from biocontrol organisms provide the necessary set of information to understand the role of evolution in invasion success (Tables 1 and 2).

Available biological control datasets

Biological control recordkeeping in the USA

There are three main stages in the process of releasing a biological control agent in the USA that may provide useful data for understanding the early phases of biological invasion: (i) importation (typically followed by a quarantine period used for host testing and nontarget studies) followed by quarantine clearance; (ii) first environmental release; and (iii) redistribution of agents from established populations within a state and across state borders (Coulson et al. 2004; Horner 2004). Each of these stages requires permitting by the United States Department of Agriculture Animal and Plant Health Inspection Service Plant Protection and Quarantine (USDA-APHIS-PPQ) and related documentation, except the within-state transfer of nonquarantine organisms (Horner 2004). The first and second stages usually involve USDA Agricultural Research Service (ARS) state quarantines, which strictly follow the permitting process. In the third stage, numerous private, local, state, and regional agencies, as well as universities become involved in the redistribution of biological control agents. Each agency has different standards for regulation, and interstate movement of biological control organisms probably occurs without proper permits. The documentation of biological control releases and establishment of agents depends on the various participating agencies and institutions. Prior to 1980, each

ARS quarantine facility, mostly involved in stages one and two, had their own forms and protocol for documentation (Coulson et al. 2004). The need for standardized documentation was realized as the number of quarantine facilities increased (Coulson et al. 2004).

A serious attempt was made in 1982 to standardize biological control recordkeeping by the establishment of the USDA ARS Biological Control Documentation Center (BCDC) (Knutson et al. 1987). The BCDC developed paper forms for recording each of the above-mentioned three stages of biological control practice to set up a uniform documentation system. The BCDC also maintains extensive records on biological control activities, mostly within the USDA, including published and unpublished reports, reprints, correspondence, journals and books relating to biological control dating back to the 1930s (Knutson et al. 1987). One of the BCDC's greatest accomplishments was the launch of an online electronic database named ROBO (Releases of Beneficial Organisms in the United States and Territories; http://www.ars-grin.gov/nigrp/robo.html). This program attempted to integrate information from participating US agencies and quarantines conducting classical biological control programs. ROBO currently provides records on importation/exportation and transfer of biological control organisms and nonindigenous pollinators for the years 1979–2008. Individual files may contain information on the original collection (e.g., shipped agents were field collected or laboratory reared, date and location of collection), initial and subsequent releases (e.g., release sites, dates, numbers of released agents), availability of voucher specimens, and much more or less depending on the given organism (Knutson et al. 1987; Table 2).

Similar databases have been, or are being, developed by various state and local agencies, universities, and individual biological control quarantine facilities or scientists. These projects differ greatly in magnitude among institutions. The BIRLDATA is an example of one of the most comprehensive databases, containing computerized records on importation, transfer and release of biological control agents received at the ARS Beneficial Insects Research Laboratory (BIRL) at Newark, Delaware from 1933 to present (L. Ertle, personal communication; Table 2). This database uses the same forms as ROBO for recording, and several entries in BIRLDATA can also be found in the ROBO database. BIRLDATA is not available online; however, copies can be requested through BIRL. The United States Department of the Interior Bureau of Land Management (BLM) also has numerous biological control release records, which are not standardized and have not been imported into any USDA database. The BLM is in the process of launching their own internal database, the National Invasive Species Information Management System (NISIMS), which will catalog biological control agent releases and other treatment types within the agency (J. Milan, personal communication).

While web-based catalogs certainly would be the most convenient way to access information on origin, numbers released, initial establishment, and recent distributions of biological control agents, the scope of the available databases do not encompass all the existing data. A plethora of printed documentation is available in the form of annual reviews, reports of local or regional agencies, catalogs, books, peer-reviewed or unpublished publications, original release forms, etc. Even though most of the documents are easily accessible through official channels (e.g., copies of historical release records from quarantines), collating all the available data on a group of organisms can be laborious depending on the details needed. More comprehensive volumes include Clausen's (1978) world review of biological control of arthropod pests and weeds. Julien and Griffiths (1998) compiled a world catalog for weed biological control agents, listing all attempts (failed or successful) undertaken in biological control of weeds up to 1996. One of the most up-to-date summaries on biological control of weeds contains information on the origin, history, and recent distributions of 94 weed biological control agents and 39 targeted weeds in the USA (Coombs et al. 2004). An updated database is underway, which will provide information on the status of weed biological control agents for the continental USA (E. Coombs, personal communication).

The above-mentioned references, along with the ROBO and BIRLDATA databases, can be useful starting points in search of the history of given biological control organisms, but the acquired data should be interpreted carefully. The catalogs rely mostly on published data, while many biological control agent importations remain unpublished (e.g., Greathead 1986), especially those considered failures (Schroeder and Goeden 1986) or if the program was unfinished (Coulson 1992). More reliable data acquisition may be ensured by focusing on states that are known to maintain extensive databases and release records and conduct intensive biological control programs (e.g., California, Oregon, Hawaii) (Coulson 1992; Coulson et al. 2004). Irregular recordkeeping is a problem for biocontrol records, including files on ROBO. The accuracy and reliability of biocontrol records often are determined by the available funding for a given program, especially the extent of monitoring establishment and efficacy after releases (Blossey 2004). Consequently, as the numbers of institutions and personnel involved in biological control increase, the quality of recordkeeping decreases.

A few additional hurdles to the utility of biocontrol data exist and must be mentioned. Though the permitting process is uniform across agencies, the permits themselves give little information on the fate of biological control agents. Additionally, the long-term monitoring of biological control agents is most often undertaken by various institutions and agencies that become involved at the third stage of releases. These agencies have independently developed different methods for recordkeeping; moreover, they are solicited but not required by law to submit their records to a national database (Coulson et al. 2004). Many agencies simply have not adopted the BCDC forms (Coulson 1992). Along with the development of ROBO, plans also were proposed to establish the US National Voucher Collection of Introduced Beneficial Arthropods (Knutson 1984). The need for such a collection has long been recognized, but this program was curtailed due to loss of technical support within the BCDC (Coulson 1992). As a result, the deposition of voucher specimens has not become centralized or regulated by the USDA or any other federal agency. Annual publications, complementary to the ROBO database, listing all biological control releases within the USA, were discontinued after 1985 due to loss of personnel and the general low priority of biological control documentation within the ARS (Coulson 1992). The situation has not improved in subsequent years; a staff of only one person is responsible for the maintenance of BCDC (G. Hanes, personal communication).

Biological control recordkeeping in Europe

The need to link data on the release of invertebrates as biological control agents across the nations of Europe is increasing (OECD 2004, Bigler et al. 2005a,b; IPPC 2005, Loomans 2007, REBECA http://www.rebeca-net.de). Several levels of standards and regulations have been given by different authorities, including the International Plant Protection Convention (IPPC), the Organisation for Economic Co-operation and Development (OECD), the European Union (EU), and the European and Mediterranean Plant Protection Organization (EPPO). A main focus in these standards is the assessment of risk of biological control agents to human health and their effects on local biodiversity. In order to obtain permission to study or release biological control organisms, a substantial amount of information is required. For example, EPPO suggests a dossier that includes a list of biological features (e.g., host plant and life history) as well as '1) details of the proposed import (amount and form of the organism, ultimate origin, immediate source); 2) whether the organism was collected from the wild (with greater risk of presence of contaminants and hyperparasites) or reared in the laboratory' (EPPO 1999). Specific guidelines on release of biocontrol organisms also suggested by EPPO include '1) the release program should be fully documented as to identity, origin, numbers/quantity released, dates, localities and any other data relevant to assessing the outcome; 2) evaluation of the releases should be planned in advance, to assess the impact of the organism on the target pest and nontarget organisms' (EPPO 2001; Table 2).

EPPO lists 91 biological control species on their webpage (EPPO 2008), which are currently used commercially in the 50 EPPO countries. It also includes a list of 43 introduced classical biocontrol agents (which may not be available commercially) in EPPO countries that have successfully established in at least one country. The information includes documentation of both successful and unsuccessful introductions, based on the BIOCAT database from CABI and some EPPO countries. This information can be used to understand differences between successful and unsuccessful introductions. Of the 43 classical biocontrol agents, 35 (81%) are documented to have been released as a single introduction within each country where they were introduced, 7 (16%) are documented to have multiple introductions into at least one of the countries where they were introduced, and one has no information. Four of the 43 species include reference to a failed establishment in at least one country where they were introduced.

Currently, there are limitations to biological control data unity and uniformity in Europe, largely due to the many, independent nations involved. First, implementation and execution of biocontrol regulation in Europe are at the national level and dependent on the national legislation. That is, international standards are not binding, although often they have been the basis for rules and standards at the national level. Nevertheless, huge differences among European countries both at the legislative and implementation levels exist (Loomans 2007). Additionally, the necessary information outlined in the international standards for biocontrol research or release does not contain a mandate to include the information in a database. This results in limited available and unified information across Europe (Loomans 2007).

Biological control recordkeeping in Australia and New Zealand

Biocontrol agents introduced in Australia must go through a government-regulated process that includes importation of the potential agent into containment, host-specificity testing, and eventual release (Harrison et al. 2005). In New Zealand, host-specificity testing is not currently formally regulated, but the Environmental Risk Management Authority (ERMA) is advising potential applicants of the importance of appropriate testing because approved applications to date typically included extensive host-specificity testing following a centrifugal phylogenetic approach (Barratt and Moeed 2005). Another difference between the two countries is that once New Zealand grants full release of a biocontrol agent, no monitoring or data collection is required by law, though postrelease monitoring is encouraged. A separate approval category called 'conditional release' in New Zealand, however, can put additional regulations on approved releases that mandate monitoring, reporting, and record-keeping (Vieglais and Harrison 2004; Barratt and Moeed 2005). In Australia, monitoring of establishment, efficacy, and any nontarget effects must be reported to the Australian Quarantine Inspection Service (AQIS) 1 year after release (Harrison et al. 2005). Finally, in New Zealand, at least a single voucher specimen of any imported potential biocontrol species is required to be deposited into the New Zealand Arthropod Collection (NZAC) (Berry 1998; http://www.landcareresearch.co.nz). This voucher system ensures the correct taxonomic identity for the imported species.

Potential improvements to biological control datasets for invasive species research

Ecologists and evolutionary biologists need to become aware of appropriate available datasets that can be used for understanding the early stages of invasion. Biological control data may provide important insights into these early stages. In order to record and store data that can be useful for future research, possibly by researchers in a different sub-discipline from classical biocontrol, data should be reliable and be as complete as possible. Useful information that can be added to these datasets includes: (i) number and sources of original collections that contributed to the founding laboratory population, (ii) the breeding colony protocols of the quarantine growth phase (e.g., inbred maternal lines versus source mixing), (iii) the number of individuals released, (iv) the location of each release, and (v) the long-term establishment and recent distribution of biological control releases (Table 1). These five pieces of information standardized across all biological control laboratories would be basic information that other researchers could use. For example, if these data were available, invasive species biologists could use these data to compare establishment success with the collection area in the native range to investigate questions relating to plasticity versus adaptation. Long-term establishment data collected by the researchers who release and monitor the biocontrol agents would allow other investigators to determine adaptation to novel conditions, particularly if the biocontrol agent has spread on its own to nonrelease areas. The documentation of establishment failures also is a priority so that comparisons of failures can be made with species or locations that successfully established. Once establishment is confirmed in the new environment and the biocontrol agents begin to spread, the importance and possible constraints of environmental factors could be evaluated. The numbers of individuals released would be useful for relating establishment success or failure to potential genetic bottlenecks or Allee effects. Ideally, all this information would be stored in national (or international), public databases that are globally accessible on the internet. Recently, there has been a proposal for and description of a new centralized database for arthropod biocontrol in the USA (Warner et al. 2009) that if implemented may help in the accessibility and utility of recorded information.

Voucher specimens are not only necessary for positive identification of biocontrol agents, but they also would be useful for evolutionary studies if they were preserved at all stages of the biological control process from original collection(s) to recovered samples after release, including periodical sampling from the laboratory colony (Huber 1998). Currently, whenever vouchers are required by regulation, they are only required in association with initial import. For example, New Zealand (http://www.landcareresearch.co.nz) and Nebraska, USA (2–10 113 of the Plant Protection and Plant Pest Act, revised 2008; accessed online: http://www.agr.state.ne.us/regulate/bpi/ent/actba.htm#top) require a deposited voucher of any potential biocontrol organism for which release approval is being sought. In addition, a few agencies keep voucher specimens of all biological control organisms that have passed through their laboratories (e.g., the ARS BIRL has vouchers since 1968, L. Ertle, personal communication; the Western Regional Research Center maintains collections, S. Swope, personal observation). Voucher collections made throughout the duration of a biocontrol program can be housed on-site at the biocontrol facility, or they could be donated to nearby museums to be curated in their collections. These specimens would provide morphological and genetic data over the time period for which little is known of the evolutionary processes involved in biological invasion.

Finally, published records, either in peer-reviewed literature or on the biological control databases, should include physiological tolerance data and laboratory-rearing conditions (see, e.g., Bush and Neck 1976). Data that would be informative in modeling establishment success in the field include such factors as optimum egg-laying temperature, temperature required for flight, and population growth rates at three or more temperatures. These data should be easily obtainable from biocontrol laboratory protocols, particularly because biocontrol laboratories have to determine appropriate temperatures for rapid rearing.

The utility of the horticultural trade in the study of the initial phases of invasion

Plants introduced via the horticulture trade share several major characteristics with introduced biocontrol organisms. Both groups are deliberately introduced, and importation records should exist in some form for both biocontrol organisms and horticultural plants. Thus, there is documentation of introduction, unlike most invasive species that arrive undetected. Both horticultural plants and biocontrol organisms are generally selected to be preadapted to the local climate of introduction and may be selected for vigorous growth and reproduction among other potentially invasive attributes (Bell et al. 2003; Mack 2005).

Differences, however, also exist. Horticultural plants are most often generalists in their biotic and abiotic requirements because they must be able to grow and thrive in a variety of soil, moisture, and/or light conditions to be commercially viable. Additionally, horticultural species span a wide range of life-history and life-form characteristics, whereas biocontrol organisms necessarily tend to be more specialized (van Klinken and Edwards 2002). Horticultural species introductions also are much more numerous than biocontrol introductions; deliberate ornamental and landscaping introductions account for the majority of naturalized and invasive plants in the USA, despite the fact that most horticultural introductions fail to escape cultivation (Reichard and Hamilton 1997; Reichard and White 2001; Mack and Erneberg 2002). The horticulture trade is an economically significant industry, which profits greatly from continual novelty (Shields and Willits 2003; Carman and Rodriguez 2004), thus introductions of new horticultural species are numerous and ongoing (Reichard and White 2001; Mack 2005). Horticultural invasions in the USA are expected to increase as ornamental plant importation from China increases (National Research Council 2002). Although both horticultural plants and biocontrol species are selected for some environmental preadaptation, a relatively small percentage of introduced horticultural plants actually escape into wildlands and become naturalized or invasive, in contrast to biocontrol species, which generally have relatively high naturalization success rates (Mack and Erneberg 2002; Hajek 2004; Mack 2005). Indeed, biocontrol agents are generally released as a population with the expectation of that population becoming self-sustaining, whereas many horticultural releases or ‘escapes’ begin with few individuals in small, isolated populations. Ultimately, however, there may not be much difference in overall propagule pressure between biocontrol agents and horticultural introductions if the horticultural species are commercially successful. In addition to ecological factors such as limited water availability outside irrigated gardens or intense competition from native and other non-native species, Allee effects, including low population density, a lack of pollinators or potentially even pollen donors, and possibly limited seed dispersal, may partially explain why so few horticultural species fail to escape cultivation. The investigation of attributes determining invasiveness is greatly improved by incorporating documented invasion failures into analyses (Kolar and Lodge 2001; Marchetti et al. 2004); as the horticulture trade provides plenty of examples of both successes and failures, it has and will continue to provide a useful system for investigating factors affecting invasion success (Table 1).

In particular, introductions from the horticulture trade can be used to investigate the evolutionary changes necessary for a cultivated species to escape and not only become established but also expand to become invasive. Morphological and genetic comparisons can be conducted between the horticultural forms and the invasive forms in order to identify differences between the groups. Once differences are identified, common garden experiments can be used to investigate evolution between horticultural and invasive forms of the same species such as variation in growth, reproduction, or competitive ability. Additionally, this line of investigation can be replicated for popular horticultural species that tolerate a large environmental amplitude by studying the same species across a geographically wide range within the introduced horticultural region. Finally, using introduction records and plant catalogs, horticultural data can be used to determine the amount of lag time for a species between introduction and expansion, and a plant’s popularity, determined by industry sales information, can provide a relative estimate of propagule pressure (e.g., Dehnen-Schmutz et al. 2007; Pemberton and Liu 2009).

Available horticulture datasets in the USA

One factor that reduces the value of horticultural plants as models for invasion is the limited regulation of the horticulture trade in the USA. This results in poor-centralized importation records and documentation. The USDA-APHIS currently inspects plant imports for only a short list of federally prohibited noxious weeds (and plant pests and pathogens) and records pest interception data for these prohibited species in the Port Information Network (PIN) database (Mack et al. 2000; Reichard and White 2001; National Research Council 2002; D’Antonio et al. 2004; Table 2). Risk assessments currently are not required for new or ongoing nursery plant importations (USDA APHIS 2004). Although APHIS requires a port of entry inspection and phytosanitary certificate for intentional plant imports, these data are not at all detailed and are for internal use only (USDA APHIS 2004; A.T. Tschanz, APHIS, personal communication). Currently, even APHIS lacks access to accurate data on plant imports because phytosanitary certificates do not require scientific plant names, but instead allow broader names for plant shipments such as 'tropical foliage' (USDA APHIS 2004). At present, researchers must look to botanical garden records and both historic and current nursery catalogs to assess importation and introduction patterns of horticultural plants. Such techniques have been employed with some success in the study of large-scale invasion processes. For example, Mack (1991) utilized the extensive Nursery and Seed Trade Catalogs Collection at the National Agricultural Library (NAL) in Beltsville, Maryland, and collections held in the Department of Special Collections at the Peter J. Shields Library, University of California-Davis, to determine the timing of introduction and scale of dissemination of common naturalized and invasive species now found in the USA. In addition, Reichard and Hamilton (1997) used pre-1930s nursery and seed catalogs to determine a wide list of early horticultural imports, which they analyzed to develop a useful predictive model and decision tree for predicting plant invaders based on species attributes. Similarly, Dehnen-Schmutz et al. (2007) used current and mid-nineteenth century nursery catalogs that provided marketing pressure values as a proxy for propagule pressure for a wide variety of horticultural species and to analyze species characteristics associated with invasiveness. Finally, a recent study that examined horticultural sales catalogs from 1887 to 1930 found a significant relationship between the number of years that a plant species was offered for sale and the probability of both establishment and invasion (Pemberton and Liu 2009).

Potential improvements to horticulture datasets for invasive species research

Major opportunities exist to improve horticultural species import datasets for evolutionary research (Table 2). Chief among these is the current APHIS review and potential amendments to nursery stock quarantine regulations covering importation of plants for planting (Quarantine 37, 7 CFR part 319; USDA APHIS 2004). Identified priority measures for revision specifically include collecting current importation data on plants. APHIS is determining 'how to best collect data on current imports of plants for planting so we can accurately ascertain the volume, type, and origin of such plants entering the United States,' and it is considering revising regulations to require this information for all nursery imports (USDA APHIS 2004). A National Research Council (2002) report on predicting invasions recommended that APHIS expand the PIN database (that currently tracks only data on prohibited plant pests) to include documentation of all imported vascular plant species; this may be an appropriate system for tracking intentional plant imports. If amendments to Q-37 include mandating detailed import data for all nursery stock, including species names, quantities, plant origin, and voucher specimens for future analysis, and those data are made accessible for scientific use, they would create an invaluable resource for studying horticultural plant invasions, particularly at the early stages of invasion, and improve risk assessment methodologies, which in turn would aid APHIS greatly in future invasive species prevention efforts. In addition, online searchable catalogs of agricultural library holdings, specifically with regard to nursery and seed catalog collections, also would be an asset for researching invasions via the horticulture industry, as multiple studies have already shown the utility of these data (e.g., Mack 1991; Reichard and Hamilton 1997; Dehnen-Schmutz et al. 2007; Pemberton and Liu 2009). The Seed and Nursery Catalog Collection at the New York Botanical Garden and the Ethel Zoe Bailey Horticultural Catalogue collection at Cornell University represent two extensive collections, in addition to the NAL and UC-Davis collections already mentioned. Holdings information about these collections of historical catalogs generally are not available online, but at least at some libraries efforts are being made toward producing searchable databases of nursery and seed catalog collections (J. Skarstad, UC-Davis, personal communication).

Experimental field trials of horticultural plants in new ranges also can significantly contribute to the scientific study of invasion biology (Mack 2005). Many commercial growers have test gardens established for evaluating new plants for production and sale. If data from such field trials were standardized and shared, it would also substantially benefit the scientific study of invasion while aiding in risk assessment and invasion prevention (Mack 2005). APHIS also is considering including field testing requirements for new plant imports as part of the aforementioned amendments to nursery stock quarantine regulations (USDA APHIS 2004). Amended regulations may require standard operating procedures for both plant exporters and importers, including plant inspection and testing, detailed recordkeeping, and small-scale field testing of plants excluded for importation pending risk assessment (if this proposed exclusion category is in fact established by regulation amendments) (USDA APHIS 2004). A best management practices program of this nature would likely include federal and/or state oversight to ensure compliance. We suspect that making such data additionally available for scientific use would be straightforward to implement.

The utility of natural history collections in the study of the initial phases of invasion

Information provided by natural history collections has been used in a number of studies examining biological invasions (e.g., Suarez et al. 2005; Zangerl and Berenbaum 2005; Phillips and Shine 2006; Ward 2007; Russello et al. 2008; Crawford and Hoagland 2009). However, considering the number of specimens available and the number of invasive species worldwide, natural history collections are a vastly underutilized resource in the study of invasion biology. One advantage of collections is that they contain usable information over a broad set of taxonomic groups not represented in either biological control or horticultural datasets. Yet collections are complementary to data from biocontrol or horticulture because of their ability to provide a historical perspective on the invasion process. This historical element is critical to understanding the early phases of invasion because introduced species are not recognized as being invasive until the expansion phase. These collections offer a unique opportunity to examine genetic variation of populations during the establishment and lag phases of invasion (Table 1). Introduced species may even be overrepresented in collections during the establishment and lag phase because of collection biases for rare and novel organisms. Natural history collections have proven useful for identifying the time frame and source of introduction, which are key factors in understanding ecological and evolutionary processes that influence the invasion dynamics of introduced species. Collections also have been useful in determining whether the establishment and early stages of invasion are linked to single or multiple introductions. For example, Russello et al. (2008) used genetic evidence obtained from natural history specimens to infer the origin of monk parakeet (*Myiopsitta monachus*) populations in the USA and to link the invasion success of this species to propagule pressure exerted by the pet trade industry.

Voucher specimens are useful for testing evolutionary hypotheses through data gathered from examination of trait and molecular variation. Molecular methods can be used to examine genetic variation of introduced populations and to reconstruct patterns of genetic change over time. For example, Hartley et al. (2006) used DNA extracted from vouchers to determine that blowflies were preadapted to rapid evolution in response to organophosphate insecticides. Also, phenotypic changes that occur during the different stages of invasions can be examined using natural history collections. Zangerl and Berenbaum (2005) used herbarium specimens to examine changes in phytochemistry of an invasive plant over a 152-year time period after introduction. In accordance with the enemy release hypothesis (Keane and Crawley 2002), they found that insect damage was nonexistent during the establishment phase of this species, and in accordance with the evolution of increased competitive ability hypothesis (Blossey and Nötzgold 1995), they found that defense compounds of plants from the introduced range were significantly lower than those of plants from the native range. Further, defense compounds increased after the accidental introduction of a specialist insect herbivore from the native range.

Another approach to examine factors that contribute to invasion success is to study a group of introduced species, both invasive and noninvasive. For example, Suarez et al. (2005) examined unintentionally introduced ant species from port-of-entry samples stored at the National Museum of Natural History. They found that 12% of 232 introduced species have become established in the USA, and that the probability of establishment was influenced by propagule pressure and nesting habit of ant species. Similar investigations of intentional introductions, such as biocontrol agents and horticultural plants (see above), also may provide important information on species-level ecological traits as well as phylogenetic patterns and evolutionary processes related to invasion success.

Natural history collection data are not quantitative and include species occurrences only (no absence data). In addition, especially when dealing with few samples, there is a concern about how representative the samples are of the introduced populations. In some cases, these concerns can be alleviated and relative abundances of invaders can be determined from passive sampling techniques that indiscriminately collect specimens (e.g., pitfall traps and port-of-entry samples). Also, relative abundances may be inferred using specimens as a random sample of the associated community. For example, changes in the composition of pollen loads collected from bumble bee specimens reflected changes in abundance of an invasive weed in northwestern Europe (Kleijn and Raemakers 2008). Similarly, insect and other animal specimens could be used to examine invasive parasitoids, parasites, and pathogens, and plant specimens could be used to examine invasive herbivores and pathogens. Despite the limitations of natural history collections, numerous studies have demonstrated the utility of these collections in the study of invasion biology.

Available natural history collections datasets

Natural history collections from museums and herbaria contain a wealth of data that may be used in the study of biological invasions. For example, Suarez and Tsutsui (2004) estimated that more than 100 million insect specimens are contained in just 11 entomological collections in the United States. Worldwide, natural history collections contain billions of specimens that have been collected over hundreds of years and these collections are continuing to grow (Lane 1996; Krishtalka and Humphrey 2000; Causey et al. 2004). Natural history collections provide a valuable source of preserved biological materials ranging from whole organisms to DNA libraries and cell lines. Collection specimens are associated with, at minimum, information on the date and locality of collection, and often have additional information, including associated observational data and physical samples derived from specimens, such as frozen tissues and DNA extracts. Furthermore, much of the data housed in natural history collections recently has been digitized and is available through a number of searchable databases and online resources. Biodiversity informatics is an emerging field of science, and great strides have been made to link available genetic, species, and ecosystem level data, and make these data available electronically to users worldwide (Bisby 2000; Edwards et al. 2000; Canhos et al. 2004; Sarkar 2007; Guralnick and Hill 2009). The Invaders Database System (http://invader.dbs.umt.edu), National Biological Information Infrastructure (http://www.nbii.gov), Global Biodiversity Information Facility (GBIF, http://www.gbif.org) are just a few examples of online data portals and resources that provide access to a global network of biodiversity information, including data on voucher specimens located in natural history collections found throughout the world (Table 2). The Invaders Database System is focused on the Pacific Northwest region of the USA and combines manually entered herbarium records dating back to 1877 with records from regional literature, extension agents, and state agriculture departments, providing presence data that allow researchers to examine historical spread. Data portals link information content and provide an infrastructure for searching a number of databases at one time. For example, GBIF provides access to 285 data providers, 7445 datasets, and nearly 175 million searchable records. Some online data sources, such as Lifemapper (http://www.lifemapper.org) and the Ocean Biogeographic Information System (http://www.iobis.org) provide links to data from a number of collections as well as tools for mapping and predicting species distributions using linked data. Such online resources will only continue to enhance the accessibility of data; however, many natural history collections are still making efforts to digitize available data. Thus, invasive species researchers should be aware that there may be a number of local, regional, and taxon-specific collections containing voucher specimens with potentially important data that are not yet summarized electronically.

Potential improvements to collections datasets for invasive species research

Improvements to natural history collection data accessibility are well underway, as many curated collections are being digitized and made available on the internet. Digitization of collection data is important for invasive species researchers who may want to use these collections, and the linking of many collections through a data portal or centralized database increases the power of available data. To facilitate the study of early-stage invasions, we recommend that researchers and field collectors, who often are very familiar with the flora or fauna within the regions they study, collect and deposit voucher specimens in the appropriate natural history collection when new or rare species are detected, in particular those species of foreign origin. Further, if an introduced species is observed in a new habitat, it would be especially useful to collect multiple individuals and to record the number of individuals observed in the population. Also voucher specimens for biological control introductions and new horticultural introductions should be deposited in the appropriate natural history collection with pertinent data, including geographic source of origin. In particular, we recommend that natural resource managers and researchers introducing biocontrol agents deposit voucher specimens with data including the number of individuals introduced, the original source population of agents, the laboratory where they were reared, and the location of introduction. Because substantial efforts are being made to digitize and link data from natural history collections through centralized data portals and databases, these vouchers may be especially useful for future investigations.

Conclusions

Understanding and combating invasive species require effective use of all available resources. Biocontrol releases, horticultural introductions, and natural history collections are three underutilized resources that can provide information to address the poorly understood ecological and evolutionary processes at the early stages of biological invasions (Table 1). We argue that biocontrol agents are good study organisms for this purpose because often life history and sample information is available from the native range or original biocontrol collections, and laboratory rearing and release records are kept. Horticultural introductions show great promise in understanding the role of evolution in the transition from introduced to invasive because they are largely generalist species and there is a continual stream of new introductions required by the industry. Natural history collections can be applied to understanding some of the evolutionary changes that may be necessary for species to become invasive by utilizing the inherent time-series element of collections data. Data from all three of these resources also may be useful in synthetic research. For example, with knowledge gained from each of these datasets researchers will be able to compare taxonomic groups (i.e., primarily insects from biocontrol, plants in horticulture, and a wide range of organisms, including pathogens, from natural history collections) to determine taxon-specific responses versus true generalities in early invasion processes.

Each of these datasets has its advantages and disadvantages. Disadvantages that stem from poorly documented or inaccessible data, however, can be corrected so that collected data are standardized and made publicly available. Such measures will only enhance the utility of these study systems for understanding the invasion process in general and the role of evolution in successful invasions in particular. These data accessibility challenges realistically can be overcome in the near future. For example, natural history collections are increasingly obtaining funding for digitizing voucher label information, and in many cases, providing digital images of the specimens online. In addition, if the USDA Quarantine 37 regulations regarding the importation of nursery plants are amended per the National Research Council (2002) recommendations, APHIS would be charged with managing data collection that would better equip them in attaining their mission of protecting against the introduction of pests. A byproduct of these regulatory changes would be an accessible resource for studying horticultural invasions. Finally, as part of approval for release of new biocontrol agents, government agencies that grant the approval could require the permit-holder(s) to make colony, release, and monitoring record data available on a centralized and publicly available database.

Acknowledgements

We would like to thank C. Lee, K. Schierenbeck, and R. Holt, organizers of 'Synthesizing Ecology and Evolution for the Study of Invasive Species,' for putting together a great meeting that spawned our collaboration. We also thank the other conference participants who provided insightful comments. We thank E. Coombs (Oregon State Department of Agriculture), J. Ertle (USDA ARS BIRL), G. Hanes (USDA ARS BCDC), and J. Milan (ISDA/BLM) for providing invaluable insider information on the present state of biological control recordkeeping. We thank S. Reichard (University of Washington) and A. Tschanz (USDA APHIS) for their insights on the current documentation of horticultural imports. We thank J. Skarstad for information on seed catalog holdings digitization. T.D.M. was funded under grants to G.N. Ervin from the US Geological Survey Biological Resources Discipline (04HQAG0135 and 08HQAG0139) and US Department of Agriculture (2007-55320-17847) during the writing of this manuscript. This work also was completed with the help of funding from the US Department of Agriculture NRI-CSREES grant 2008-35302-04680 to N.D.T. and from the Academy of Finland (project 118456) to L.L. We thank A. Caesar, D. Kazmer, and K. Rice who commented on an earlier draft of the manuscript and two anonymous referees who provided valuable suggestions that improved the study.

Authors' contributions

All authors contributed to the ideas addressed in the manuscript. T.D.M., as lead author, compiled and edited written contributions from J.W.B., E.K.E., M.A.J., L.L., and M.S. G.W.G., G.K.R., and N.D.T. contributed additional revisions to the manuscript.

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