

# Biodiversity, ecosystem functioning, and classical biological control

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**Abstract** Increasing concern over worldwide loss of biodiversity has led ecologists to focus intently on how ecosystem functioning may depend on diversity. In applied entomology, there is longstanding interest in the issue, especially as regards the importance of natural enemy diversity for pest control. Here I review parallels in interest, conceptual framework, and conclusions concerning biodiversity as it affects ecosystem functioning in general and classical biological control in particular. Whereas the former focuses on implications of loss of diversity, the latter focuses on implications of increase in diversity as additional species of natural enemies are introduced to novel communities in new geographic regions for insect pest and weed control. Many field studies now demonstrate that ecosystem functioning, e.g., as reflected in primary productivity, is enhanced and stabilized over time by high diversity as the community increases in its efficiency in exploiting available resources. Similarly, there is growing field support for the generalization that increasing species and functional diversity of natural enemies leads to increasing pest suppression. Nonetheless a central concern of classical biological control in particular, as it seeks to minimize non-target effects, remains as to whether one or a few species of natural enemies can provide sufficient pest control.

**Keywords** Ecological redundancy · Niche partitioning · Species complementarity · Species introductions · Squarrose knapweed

## Introduction

The importance of biodiversity as it affects interactions of plants, herbivores, and carnivores has a long and distinguished history in applied entomology and zoology (e.g., Pimentel 1961; Root 1973). One arena in which it has been a central topic is the practice of classical biological control of insect pests and weeds, wherein natural enemies from a pest's native range are introduced to new geographic regions where the pest has become problematic (Huffaker et al. 1976). The effort is founded on the premise that an absence of natural enemies allows the pest to grow to large numbers in its new range. A fundamental issue in the practice, long debated and still awaiting final resolution, is the question of how diverse the community of introduced natural enemies should be: should practitioners introduce one, a few, or many species of natural enemies against the pest? In other words, should the goal be to build a more diverse or less diverse community of natural enemies to attack the pest in its new geographic range?

Pest control is one of many ecosystem services that ecologists increasingly are focusing upon as influenced by biodiversity (Cardinale et al. 2012; Hooper et al. 2012). There are strong parallels of interest, conceptual grounding, and conclusions emerging from consideration of the importance of biodiversity in ecosystem functioning in general, and in the applied practice of classical biological control in particular. This brief review of both the recent explosion of interest concerning ecosystem functioning in general, and the longstanding interest concerning classical biological control in particular, is intended to highlight these parallels. I begin by considering biodiversity and ecosystem functioning in general and then shift to considering biodiversity and the practice of classical biological control in particular.

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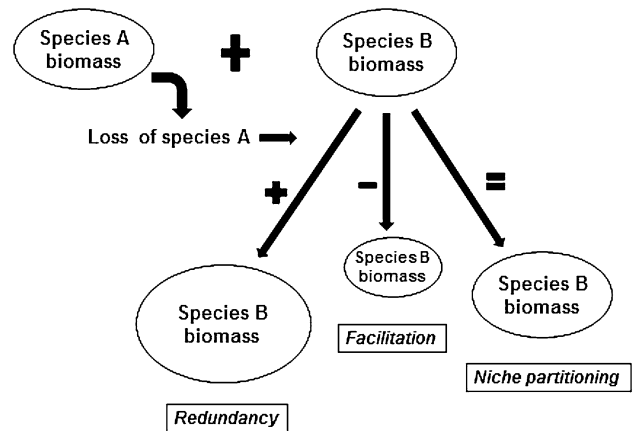
## How does biodiversity influence ecosystem functioning?

One fundamental feature of ecological communities is the diversity or number of species that are found living together at any one place. Ecologists have focused intently for many decades on what determines the variation in species diversity among communities, as in the general pattern of decreasing diversity as one moves away from the equator and the tropics (Schemske et al. 2009; Wiens 2011).

Over the past 25 years, ecologists' interest in species diversity has expanded and shifted as well to include determining the significance of diversity at any one place for the functioning of the ecosystem (i.e., the flow of energy and cycling of nutrients) that includes that local community. This recent focus emerged especially in the 1980s as ecologists viewed with great alarm shrinking biodiversity (e.g., Ehrlich and Ehrlich 1981; Ehrlich and Wilson 1991). Ecologists by the early 1990s were becoming increasingly focused on determining the significance of biodiversity for such ecosystem functions as “soaking up carbon dioxide, preserving soil fertility, controlling pest outbreaks, retaining water, among many others” (Baskin 1994). Movement forward was propelled by the 1992 Earth Summit of world governments in Rio de Janeiro (Parson et al. 1992), and by international collaboration on ecosystem function of biodiversity that included a symposium held in Germany in 1991. From the symposium came publication of a major synthesis volume addressing the state of knowledge and new frontiers concerning the topic (Schulze and Mooney 1993).

Ecologists have considered the importance of biodiversity for many ecosystem functions (e.g., Cardinale 2011; Carey and Wahl 2011; Handa et al. 2014). In particular, the importance of biodiversity for primary productivity has received especially high levels of attention and field testing over the past quarter century (Cardinale et al. 2011, 2012; Hector et al. 2010; Hooper et al. 2005; Tilman et al. 2001). This focus on effects of diversity on productivity of a plant community at a given site complements ongoing research on global patterns (i.e., across plant communities) of species diversity as influenced by site productivity (Fraser et al. 2015; Grace et al. 2014). Conclusions emerging from synthesis of primary productivity research are focused on here, as they serve well to illustrate the importance of biodiversity for many ecosystem functions.

In the context of worldwide biodiversity loss, the key question asked in studies of biodiversity and primary productivity can be posed as: how will remaining species of plants respond to the loss (e.g., experimental removal) of a species from a community? Three general ecological mechanisms (niche partitioning, competition, and facilitation)



**Fig. 1** In a simple community of two plant species A and B, removal (loss) of Species A can lead to an increase in the biomass produced by Species B (i.e., there is competition and redundancy in the community); no change in the biomass produced by Species B (as may happen if there is complete niche partitioning); or a decrease in the biomass produced by Species B (which is facilitated in its growth by the presence of species A)

may govern the community's response. These can be illustrated most simply by considering a community of just two plant species A and B (Fig. 1). One can imagine that species A is either removed altogether experimentally, or that its productivity is reduced naturally by growing conditions (e.g., drought) in a given year. Will species B increase in its productivity such as to compensate for the loss of species A? If there is very strong niche partitioning between the two species, the removal of species A may have minimal effect on the productivity of species B. Hence community productivity (i.e., the combined productivity of species A and B) may decline. On the other hand, if there is strong competition between the two species, the removal of species A may result in increased productivity of species B, and therefore in compensation to some degree (which can range from partial to over compensation) in community productivity. Compensation can be said to arise from ecological redundancy (Hooper et al. 2005; Naeem and Li 1997) tied to competition in the contributions of the two species to their combined (community) productivity. Finally, if species A facilitates the productivity of species B when they occur together (e.g., only species A may fix nitrogen), the removal of species A may result in reduced productivity of species B, and hence even greater reduction in community productivity than would occur with only strong niche partitioning.

Ecologists all over the world during the past 25 years have conducted experiments to address the net and relative importance of these three ecological mechanisms in determining the response of community productivity with the loss of individual plant species. Expectations and

predictions in these experiments have been influenced by key insights early in the development of the sciences of evolution and ecology. Darwin (1872) recognized clearly the potential importance of biodiversity in enhancing primary productivity (McNaughton 1993). Darwin described as the ultimate result of sustained interspecific competition over time, that natural selection can drive closely interacting species to diverge from one another in their use of resources such as to lessen the severity of competition among them. Such divergence (i.e., niche partitioning) inevitably involves the concept of trade-off, wherein a species increases its efficiency at exploiting some subset of resources necessarily at the cost of decreased efficiency concerning other subsets of resources (e.g., Tilman 1993). Darwin surmised further that as a natural consequence, more of the resources available would be used when more species were present, and hence community productivity would increase with species diversity [as expressed currently, the efficiency of resource use by the community and hence productivity would be greater as the result of species complementarity (Cardinale et al. 2007; Hooper et al. 2005; Loreau and Hector 2001)]. The theoretical foundation of the importance of such niche divergence and partitioning for the maintenance of species diversity and for its potential enhancement of community productivity has been explored extensively (Chesson 2000; Yachi and Loreau 2007).

The importance of species diversity for ecosystem functioning was also emphasized by others as the field of ecology developed. In particular, Elton (1958) and MacArthur (1955) proposed influentially that greater species diversity results in greater stability of communities, and by extension (and as phrased in the language of today), of ecosystem functioning over time (e.g., as reflected in reduced variability in the amount of primary productivity from year to year). Stability of ecosystem functioning occurs in diverse communities even as populations of individual species fluctuate in size and impact over time. Thus the growing conditions of one year may promote increased population response by some species and decreased response by others (including tilting competition in favor of one species over another). Consequently the community as a whole more fully and consistently exploits over time the resources available than would a single species that is continually buffeted by varying growing conditions from year to year. Hence there is greater ecosystem reliability that arises from the biological insurance associated with species-rich communities (Naem and Li 1997; Yachi and Loreau 1999). One intriguing hypothesized consequence of such community stability is Elton's (1958) concept of biotic resistance: greater species diversity in a community leads (through fuller resource use at all times) to increased resistance to invasion of the community by new species.

The importance of species diversity for community and ecosystem stability has been further explored and elucidated from a theoretical approach. May (1974, 2001) demonstrated that increasing species richness and trophic complexity leads generally to greater fluctuations in population size of individual species, yet at the same time tends to stabilize (reduce fluctuation in) the total number of individuals of all species combined. Replacement of randomly distributed species interaction strengths within communities with primarily weak interaction strengths (as may better characterize natural communities) can enhance general stability in the sense of also dampening population fluctuations of individual species, which in turn can reduce rates of species loss and conserve local diversity (May 1974, McCann 2000). Ecosystem stability derives from food-web properties and dynamics that transcend single trophic level interactions (May 1974, McCann 2000); such stability may hinge critically on consumers' short-term adaptive responses to changes in resource availabilities (Kondoh 2003).

The early insights in the development of the fields of evolution and ecology noted here became major subjects of interest right from the start with the explosion of interest and experimental testing in biodiversity-ecosystem functioning that began late in the twentieth century (Naem et al. 1994; Tilman and Downing 1994). Thus much of recent efforts have focused on the relationships of diversity-productivity as suggested by Darwin et al., and of diversity-stability as suggested by Elton et al. Also from the start ecologists recognized that, as members of a community, individual species would differ in the magnitudes and nature of their contributions to general relationships of diversity and ecosystem functioning, as for example in the recognition of keystone species and functional groups exhibiting key traits (e.g., nitrogen fixers) (Schulze and Mooney 1993). Furthermore, the importance of diversity for ecosystem functioning was recognized to extend not only to levels beyond individual species (e.g., trait and functional group diversity) but also to levels within species (e.g., genetic diversity; Hobbie et al. 1993). Thus much of the experimental effort over the past 25 years has focused on determining the extent to which diversity per se on the one hand, and the inclusion of key species within a community on the other [referred to often in the context of experimental design as the sampling effect (e.g., Hooper et al. 2005; Huston 1997; Loreau and Hector 2001; Tilman et al. 2001)], is each responsible for emergent relationships of biodiversity-ecosystem functioning (Cardinale et al. 2011, 2012; Hector et al. 2010).

Many experimental studies have been conducted in recent years to address these fundamental questions and issues concerning the effects of biodiversity on ecosystem functioning, and in particular on primary productivity. In

considering broad conclusions, I focus here on the very large body of results addressing species diversity [i.e., richness] in particular (ecologists continue to evaluate whether focus on genes, phylogeny and traits in addition to or instead of simply species number gives even clearer resolution of the importance of biodiversity for ecosystem functioning; e.g., Cadotte et al. 2008; Flynn et al. 2011; Hughes et al. 2008; Tilman et al. 1997; Tomimatsu et al. 2014; Venail et al. 2015). Among the most ambitious and impressive of such studies have been large scale manipulations of local species richness wherein varying numbers of plant species have been seeded into field plots and the resultant communities and local ecosystems have been followed over multiple years (Allan et al. 2013; Isbell et al. 2009; Reich et al. 2012; Tilman et al. 2001, 2006). Syntheses of results from these and many other studies reveal that the contributions of species collectively (species diversity per se) and individually (key species) are roughly equal in magnitude in yielding clear, overarching patterns of increased productivity and increased stability of productivity over time with increasing species diversity (Cardinale et al. 2011, 2012). The experiments thus demonstrate that species loss from an ecosystem on average results in reduced primary productivity and less stability in such productivity over time.

These general conclusions reinforce that co-occurring species in local ecosystems generally are limited in the ability to compensate for each other's loss [redundancy occurs but with limits, as communities appear characterized primarily by weak species interactions (McCann 2000)]. Niche divergence and facilitation seemingly play key roles in productivity dynamics along with the interspecific competition that underlies compensation following the loss of individual species. Niche divergence of course need not arise necessarily from past competition generating niche partitioning. Individual species may have followed evolutionary paths largely independently of the species with which they presently occur. Stability of community productivity for example could arise simply from the statistical averaging of individual responses of non-interacting species over time (the portfolio effect; Doak et al. 1998; Tilman et al. 1998). But alternatively niche divergence may indeed reflect "the ghost of competition past" (Connell 1980). It is intriguing therefore that the resolution of biodiversity-productivity relationships today may parallel and follow the earlier resolution of the importance of present-day versus past competition in determining species composition and structure of local communities (Connell 1983; MacArthur 1972; Schoener 1983).

Experimental studies have typically revealed an asymptotic relationship between biodiversity and ecosystem productivity: the reduction in productivity becomes increasingly pronounced as more species are lost (Cardinale et al. 2011, 2012), as might be expected with the increasing

importance of each individual species as fewer remain to compensate for the loss of others. A striking and thought-provoking result of long-term experimentation in Minnesota grasslands, however, is that the relationship between biodiversity and productivity has become more linear with time (Reich et al. 2012). This may reflect that effects of species complementarity have accumulated over the course of the experiment along with an increase in soil nitrogen that has occurred most strongly in species-rich plots (Reich et al. 2012). Recent research suggests another, equally intriguing and important possibility. Zuppinger-Dingley et al. (2014) demonstrated rapid development of niche partitioning between plant species when grown together (versus individually) for 8 years in the Jena (Germany) large-scale field experiment addressing biodiversity-ecosystem functioning (Allan et al. 2013). As Darwin envisioned in general but as emerged over an astonishingly short period of time in the study by Zuppinger-Dingley et al. (2014), this niche partitioning was associated with greater increase in community productivity among progeny of individuals from mixture (versus monoculture) field plots when pairs of species were grown together versus singly in the greenhouse. This study nicely illustrates how competition both present and past, as combined in complex, often surprising ways, can act to influence biodiversity-ecosystem function relationships.

Collectively, the very large number of studies completed to date demonstrate the importance of biodiversity in promoting primary productivity and other ecosystem functions (Cardinale et al. 2012; Isbell et al. 2011), and the importance of biodiversity loss to global changes in ecosystem processes (Hautier et al. 2015; Hooper et al. 2012). Many of the issues explored in these studies of biodiversity have been explored also in the literature on predator-prey interactions, although with some differences in emphasis on additive versus indirect and non-additive interactions (Ives et al. 2005). As discussed next, in particular many of the issues have been addressed in the literature devoted specifically to pest management by classical biological control.

### **How does biodiversity influence classical biological control?**

A longstanding issue in classical biological control, as noted above, has been whether to introduce many or few species of natural enemies to suppress pest numbers in a new geographic region where a pest insect or weed has become established and problematic (Ehler 1990; Huffaker et al. 1976; Kakehashi et al. 1984; Matsumoto et al. 2003; Takagi and Hirose 1994). In addressing this issue, biocontrol practitioners have considered and examined the merits of natural enemy diversity per se versus the key importance



of individual species, just as ecologists have in recent years in addressing even more generally how biodiversity affects primary productivity and other ecosystem functions. Elton (1958) and Pimentel (1961) were among early proponents stressing that more diverse communities of natural enemies provide stronger, more stable control of insect pests, a theme applied to classical biological control in particular (Huffaker and Messenger 1964; Smith 1929). Closely linked is the concept of cumulative stress in classical biological control (Denoth et al. 2002) wherein successful suppression of the target pest derives from the integrated contributions of multiple introduced species of natural enemies drawn from diverse functional groups, aptly referred to in this context as feeding guilds (Denoth et al. 2002; Harris 1985; Malecki et al. 1993; McEvoy and Coombs 1999). The concept of cumulative stress includes varying contributions of individual species across the range of conditions supporting the pest (Huffaker and Kennett 1966; Huffaker et al. 1976), and the abilities of these species to aggregate by dispersing to sites where pest numbers are increasing (Evans 2015; Kareiva 1990; Schellhorn et al. 2014). The model is based on concepts of niche partitioning, biological insurance, and complementarity as emphasized in the literature on biodiversity and ecosystem functioning discussed above.

An alternative line of thought is that a single introduced species of natural enemy has often proved sufficient in having large suppressive effect on a pest (Denoth et al. 2002; Myers 1985; Myers et al. 1989; Turnbull and Chant 1961). Many biocontrol practitioners released multiple species of natural enemies nonetheless, motivated and guided more by a lottery model (Denoth et al. 2002; Myers 1985) than a cumulative stress model. The essence of a lottery model was described by Ehler and Hall (1982, p.4): “At present, the most common strategy is to introduce all suitable natural enemies and hope that the “best” species or combination of species will be sorted out in the field.” This parallels the sampling effect as described in the field experimental literature on biodiversity and ecosystem functioning.

The lottery approach to practicing classical biological control was inherently unsatisfying in its lack of theoretical underpinning and correspondingly in its insufficient attention to determining a priori which natural enemies potentially could have greatest suppressive effect on the pest (e.g., Ehler 1990; Ehler and Hall 1982; McEvoy and Coombs 1999; Myers et al. 1989; Takagi and Hirose 1994; Turnbull and Chant 1961). Recently it has come under scrutiny also as biocontrol practitioners have sought to minimize risk of non-target effects (Denoth et al. 2002; Louda et al. 2003; McEvoy and Coombs 2000). Another fundamental concern over undesirable ecological effects of introducing multiple species of natural enemies was proposed early on. In focusing on negative interactions among

competing natural enemies, researchers hypothesized that a natural enemy less effective in suppressing a pest could out-compete a more effective natural enemy, thereby undercutting the strength of the biological control program (Ehler and Hall 1982; Pemberton and Willard 1918; Turnbull and Chant 1961; see Cardinale et al. 2011 for similar arguments applied to competition among plants and diversity-productivity relationships). One form of competition emphasized in recent years is intraguild predation, wherein natural enemies kill and consume each other as well as the pest (Polis et al. 1989; Polis and Holt 1992) thereby potentially leading to reduced effectiveness of biological control with increasing natural enemy diversity (Prasad and Snyder 2004; Rosenheim et al. 1995; Snyder and Ives 2001).

Thus, just as in the literature addressing ecosystem functioning in general, the literature of classical biological control in particular has also been filled with debate over consequences of more versus less biodiversity. Whereas the emphasis is on species loss in natural communities in the former, the emphasis is on species addition in synthetic communities (in new geographic regions) in the latter. Such species addition should in any case be done conservatively with due deliberation, given the threat of adverse non-target effects (McEvoy and Coombs 1999, 2000). It may be quite unwise furthermore to create highly diverse communities of introduced natural enemies to attack a pest if the biocontrol agents tend more to undercut each other through competition and other negative interactions than to interact positively in complementary fashion. Case studies are accumulating that address the outcomes of multiple introductions of natural enemies against a target pest. I present one such case study below of outcomes of natural enemy diversity, with emphasis on large scales of space and time.

### A case study in biological control of weeds

Introduced from Eurasia to North America, squarrose knapweed (*Centaurea virgata* Lam. ssp. *squarrosa* Gugler, Asteraceae) has become a weed of major concern in west central Utah since its first detection near Eureka in Juab County in 1928 and its subsequent spread over thousands of hectares of rangeland in the surrounding west desert of Utah (Roché and Roché 1989). The weed is a thickly branched, long-lived perennial that reproduces only by seed (Story and Woods 2004). Large individuals (up to a meter in both height and diameter) produce hundreds of flowers over the summer, each of which can yield one to seven mature seeds. By the early 1990s, a coalition of federal, state and county land managers and weed control specialists had implemented an integrated pest management (IPM) program against the weed in west central Utah, including application of herbicides, cultural techniques

(tillage and fire), and biological control. Long distance dispersal of knapweed by seed to new habitat was especially worrisome. Seed heads of squarrose knapweed bear recurved bract tips that readily attach to mammals (and to the undersides of vehicles) that thereby can serve to disperse the seeds widely; sheep grazing in the west desert is especially problematical in this regard (Roché et al. 1992). The aim of biological control efforts against squarrose knapweed hence was focused on reducing seed production in well-established stands to reduce the potential for spread through long-distance seed dispersal (smaller, isolated stands of the weed correspondingly were treated with herbicide to steadily contract the area of infestation).

In the first phase of the biological control effort, two species of seed-feeding flies, *Urophora affinis* Fraenfeld and *Urophora quadrifasciata* (Meigen) (Diptera: Tephritidae), were introduced as biological control agents to populations of squarrose knapweed beginning in the early 1990s. Along with a number of other biocontrol agents (Wilson and Randall 2001), these two species had been widely released previously in northwestern North America on spotted and diffuse knapweed (*C. stoebe* spp. *micranthos* [Gugler] Hayek and *C. diffusa* Lamarck), and *U. affinis* had become especially abundant on these two knapweed species (Story et al. 1992). On squarrose knapweed in Utah, however, *U. affinis* failed to establish while *U. quadrifasciata* became very abundant by the late 1990s (Rieder et al. 2001). Additional studies are called for to determine the mechanisms underlying this differential use of the three knapweed species by the two fly species in western North America; while it may derive in part from resource-based competitive exclusion, it could also derive from reproductive interference (Kishi et al. 2009; Nishida et al. 2015; Noriyuki et al. 2012).

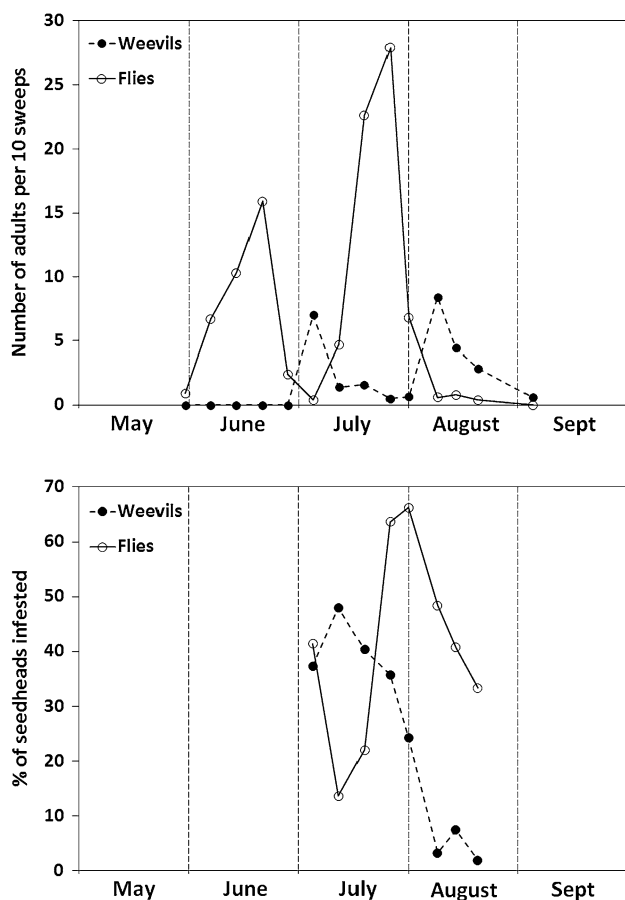
Mature larvae of *U. quadrifasciata* overwinter in galls formed from ovary wall tissues (Harris and Myers 1984). Individuals emerge as adults early in the summer (Story et al. 1992). Females lay their eggs in immature flower heads and produce a partial (non-obligatory) second generation, with summer-emerging adults exploiting flowers at sites with late season precipitation; *U. quadrifasciata* is a strong disperser that can reach isolated plants of the weed in remote locations (Harris 1985; Story et al. 1992, 2008). Populations of the fly grew quickly throughout the area of squarrose knapweed infestation in the west desert of Utah. Dissections of mature seed heads (100–500 per site) collected in late summer from multiple, widely scattered sites revealed that on average 40 % of seed heads were infested with the fly during 1996, 1997 and 1998, with up to six larvae (but most often only a single larva) infesting an individual seed head (Rieder et al. 2001).

Beginning in the late 1990s, another seed-feeding insect narrowly restricted to knapweeds (Jordan 1995), the weevil *Larinus minutus* Gyllenhal (Coleoptera: Curculionidae),

was introduced onto squarrose knapweed in west central Utah. The weevil overwinters as an adult in or on the soil in stands of knapweed, and females lay eggs in newly opened flowers to produce a single generation each year (Kashefi and Sobhian 1998; Lang et al. 1996). Although more than one egg may be laid in a squarrose knapweed flower, only a single larva matures in the seed head. As the larva feeds on and destroys all developing seeds within the seed head (Kashefi and Sobhian 1998), it also consumes fly larvae that had hatched previously and co-infest the seed head (Bourchier and Crowe 2011; Seastedt et al. 2007; Smith and Mayer 2005). There was concern therefore at the time of initial weevil releases on squarrose knapweed that this new biological control agent would undercut the effectiveness of the fly, and this might even reduce overall seed destruction by insects throughout the area of infestation. Of particular concern was that the larvae of *U. quadrifasciata* within their thin-walled galls would be highly vulnerable to intraguild predation by weevils (much more so than larvae of *U. affinis* that would be better protected within their thick-walled, woody galls in the larger seed heads of diffuse and spotted knapweed; Harris 1989). Thus interspecific competition between *Urophora* and *Larinus* might be even more detrimental to biological control of squarrose knapweed than of spotted and diffuse knapweed (Crowe and Bourchier 2006; Smith and Mayer 2005).

As it turned out, the fly and weevil have combined to attack a higher percentage of seed heads of squarrose knapweed over the past two decades than the fly alone attacked previously. In the years following initial releases, numbers of the weevil increased rapidly throughout the area of knapweed infestation in Utah's west desert. At sixteen sites sampled annually during 2009–2014, on average two-thirds of mature seed heads collected in late summer were infested by weevils and flies. Weevils accounted for most seed destruction, infesting 64 % of seed heads. Associated with such high infestation rates, weevil predation indeed appears to have reduced the formerly high fly abundance throughout the region of infestation. Percentages of seed heads in which flies succeed in maturing nonetheless seemingly have stabilized, albeit at low numbers. Thus, in 2009–2014 flies escaped intraguild predation in infesting an overall mean of nearly four percent of mature seed heads, with yearly infestation rates varying between one and seven percent and with no significant long-term trend in infestation rate over the six-year period. Studies of interactions of *Urophora* with *Larinus* over the same time span elsewhere in western North America similarly indicate that these seed-feeders co-exist in attacking diffuse and squarrose knapweed as well (Bourchier and Crowe 2011; Myers et al. 2009; Seastedt et al. 2007; Story et al. 2008).

As indicated from field data discussed next, the long-term coexistence of the fly and weevil despite intraguild



**Fig. 2** The mean number of adult flies (*U. quadrifasciata*) or weevils (*L. minutus*) collected per ten sweeps (in ten sets of ten sweeps with a 38 cm diameter net) of knapweed foliage on given dates in 2001 at a local population of squarrose knapweed near Eureka, Utah (*top*), and the percentage of open knapweed flowers marked on those dates that subsequently were infested as seed heads with flies and weevils (*bottom*)

predation appears to arise principally through differences over time and space in oviposition by the two species. These differences limit co-occurrence of the two species in individual seed heads. Correspondingly, because the two species overlap only partially in the subsets of seed heads they exploit, the two species combined inflict greater seed destruction across time and space than would either occurring alone.

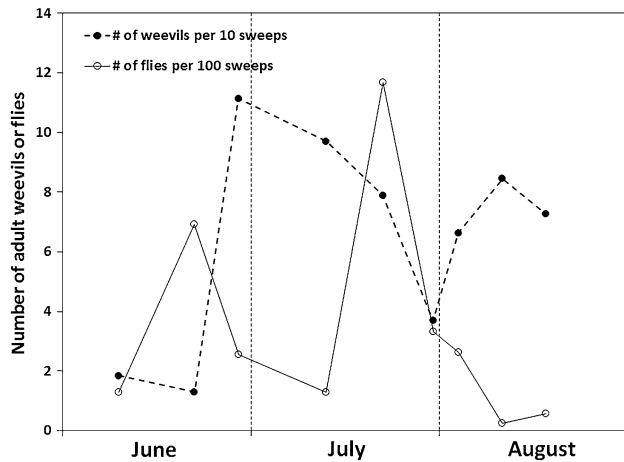
The fly and the weevil differ in their phenology as associated with squarrose knapweed, as illustrated from tracking their populations at a study site near Eureka, Utah in 2001. The seasonal abundance of adults of the two species was determined by sampling the knapweed foliage with 100 sweeps of a net once a week at the site from late May through early September (Fig. 2). The overwintering generation of flies (emerging as adults) peaked in abundance in mid to late June, while their adult offspring peaked in

abundance in late July. Weevils were delayed in phenology relative to flies. The low numbers of overwintering weevil adults present in 2001 peaked in abundance in early July and their adult offspring peaked in abundance in early August.

Seasonal patterns of infestation of knapweed seed heads by immature flies and weevils were studied also at the Eureka study site in 2001 (Fig. 2). Once flowering began at the site in early July, up to 200 open flowers were marked at each weekly visit by tying a five cm string (with distinctive color for each week) around the pedicel. These marked flowers were collected as mature seed heads 4–6 weeks later and were dissected in the laboratory to determine their contents. The seasonal pattern of percentage of seed heads infested with flies mirrored the seasonal pattern of adult abundance, with greatest percentages of seed heads infested arising from flowers that bloomed in early and late July. Although seasonal patterns of seed head attack by weevils overlapped with those of flies, the peak percentage of seed heads infested with weevils was associated with flowers that bloomed in mid-July. Thus the flies most frequently escaped intraguild predation over the course of the growing season in attacking early and late blooming flowers that in turn most frequently escaped attack from weevils. This is similar to the escape through differing phenology observed for *U. affinis* in its interactions with *L. minutus* in attacking diffuse knapweed in British Columbia (Bourchier and Crowe 2011).

As the abundance of weevils increased enormously throughout the area of knapweed infestation in central Utah during the early 2000s, correspondingly the abundance of flies decreased. Frequent sweep sampling at multiple sites throughout the summer of 2010, however, again reflected the same basic seasonal patterns of adult abundance of the two biocontrol agents: peaks in abundance of adult flies occurred in late June and late July, and of adult weevils in early July and mid-August (Fig. 3).

The weevils and flies differed not only in their abundance relative to each other at different times over the growing season in individual populations of knapweed, but also in their relative abundance spatially among host plant populations in any given year. For example, mature seed heads were sampled from large numbers of local populations of knapweed throughout west central Utah in August in 2006–2008. Laboratory dissections revealed that the overall percentages of seed heads infested by flies and weevils over the course of the season varied greatly among sites in each year, with an overall trend of decreasing percentages of seed heads infested by flies from 2006 to 2008 and increasing percentages infested by weevils (Fig. 4). Rates of seed head infestation by the fly and weevil were not significantly correlated with each other among sites in 2006 and 2008, however, and were only loosely correlated (positively) with each other in 2007 (Fig. 4). Thus, the local intensities of attack by flies and weevils were largely independent of each



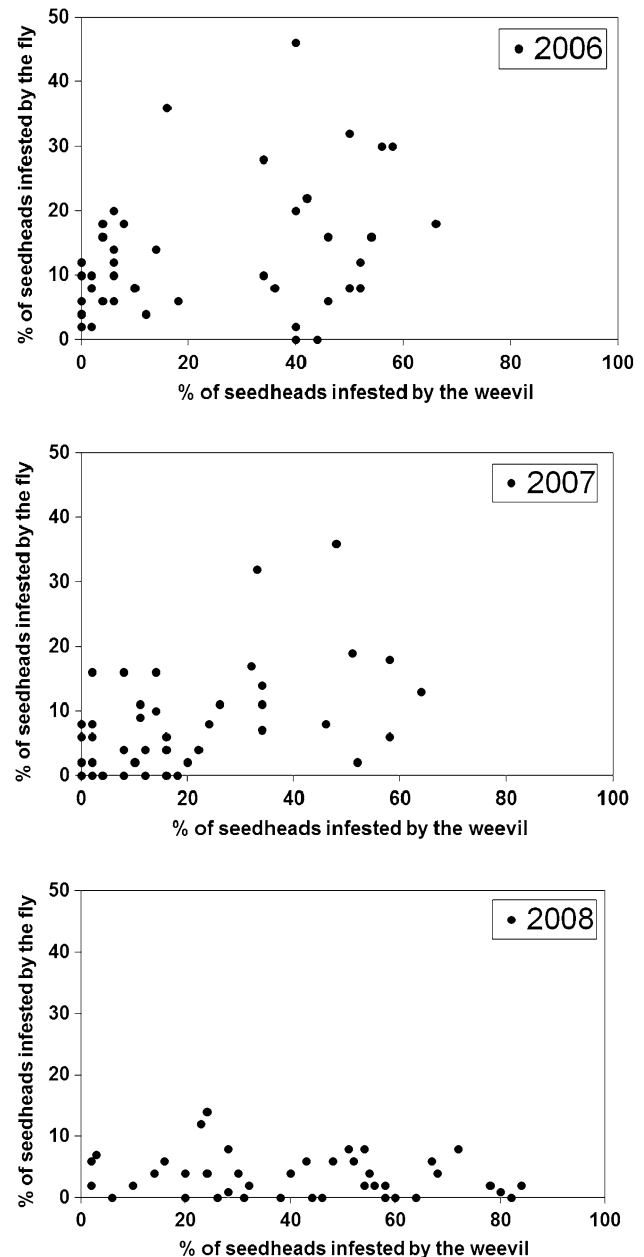
**Fig. 3** The mean number of adult flies (*U. quadrifasciata*) per one hundred sweeps or weevils (*L. minutus*) per ten sweeps of knapweed foliage in multiple local populations of squarrose knapweed along 25 km of gravel road west of Vernon, Utah, on various dates in 2010 (six sets of ten sweeps were taken at each of the 7–26 widely scattered, local populations of the weed that were sampled on any given sampling date)

other among knapweed populations scattered across west central Utah. The annually shifting and differing spatial patterns of where across the landscape weevil and fly attacks are most concentrated may contribute, along with phenological differences between the two species, to persistence of the fly even as the weevil has become very abundant.

These long-term observations of these two seed-feeding insects indicate that across the large expanse of west central Utah infested by squarrose knapweed, the fly now coexists with the weevil, albeit occurring at much lower density than prior to the weevil's introduction. Despite its reduction in numbers from weevil predation, the fly continues to contribute towards seed destruction and does so in particular by attacking seed heads that otherwise would escape over time and space from the weevil. Hence together the weevil and fly consume more knapweed seeds across the large area of weed infestation than the weevil can alone, and did the fly alone prior to the introduction of the weevil. Despite the occurrence of strong intraguild predation, the combined impact of weevil and fly demonstrates complementarity in the sense of the biodiversity-ecosystem functioning literature, in that the resource is consumed with greater efficiency (i.e., more of the available knapweed seeds each year are destroyed by insects).

### Concluding remarks

Complementarity emerges under natural conditions at very large spatial and temporal scales in the observational study



**Fig. 4** The percentages of mature seed heads ( $n = 100$ ) in each of 40–45 widely scattered, local populations of squarrose knapweed in west central Utah that were infested by the fly *U. quadrifasciata* (y axis) and by the weevil *L. minutus* (x axis) in August 2006 (top;  $r = 0.29$ ,  $p > 0.05$ ), 2007 (middle;  $r = 0.45$ ,  $p < 0.004$ ), and 2008 (bottom;  $r = -0.15$ ,  $p > 0.05$ )

of insects attacking weed seeds in the Utah desert discussed above. Similar increases in pest suppression with increasing natural enemy diversity have emerged often as well in experimental studies conducted at necessarily smaller spatial and temporal scales (e.g., Losey and Denno 1998; Snyder et al. 2006; Stephens and Myers 2014; Van Hezewijk and Bouchier 2012). Complementarity is not



always apparent, however, in such experimental studies (e.g., Evans 1991; Ferguson and Stiling 1996, Milbrath and Nechols 2014). A priori, complementarity might be expected to emerge most clearly and most consistently as temporal and spatial scales are expanded (thereby giving more opportunity for consequences of diverse aspects of niche partitioning to emerge; e.g., Huffaker and Kennett 1966; Takagi and Hirose 1994). This point has been stressed also in the biodiversity-ecosystem functioning literature (Cardinale et al. 2011, 2012; Isbell et al. 2011; Reich et al. 2012). The commonality of this theme is yet another illustration of the strong parallels in conceptual grounding associated with evaluating the importance of biodiversity in ecosystem functioning in general, and in the applied practice of classical biological control in particular.

There is commonality as well in emergent conclusions; increasing diversity of natural enemies generally appears to result in greater and more stable pest control just as increasing diversity per se generally also is associated with greater ecosystem functioning more broadly (e.g., higher and more stable primary productivity). Nonetheless, the application of such insights can differ in conservation biology (to preserve ecosystem functioning) versus in classical biological control (to achieve pest suppression with minimal non-target effects). A key issue to be addressed case by case in classical biological control is whether sufficient (versus maximum) pest control can be achieved by a single or few introduced species of natural enemies. This may or may not be the case, given that even specialist species of natural enemies may have evolved in their life histories (e.g., phenology, habitat preferences, or requirements for oviposition and/or development) such that they effectively attack only a subset of the target pest population. The issue of how many biocontrol agents may be required for adequate rather than maximum pest control highlights differences in goals and concerns associated with striving to prevent species loss from presently existing communities (as addressed by study of biodiversity-ecosystem functioning in general) and of striving in classical biological control to create new communities of introduced natural enemies to attack invasive pests.

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