

Critical Review

The Role of Source-Sink Dynamics in the Assessment of Risk to Nontarget Arthropods from the Use of Plant Protection Products

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Abstract: The concept of source-sink dynamics as a potentially important component of metapopulation dynamics was introduced in the 1980s. The objective of the present review was to review the considerable body of work that has been developed, to consider its theoretical implications as well as to understand how source-sink dynamics may manifest under field conditions in the specific case of nontarget arthropods in the agricultural environment. Our review concludes that metapopulation dynamics based on field observations are often far more complex than existing theoretical source-sink models would indicate, because they are dependent on numerous population processes and influencing factors. The difficulty in identifying and measuring these factors likely explains why empirical studies assessing source-sink dynamics are scarce. Furthermore, we highlight the importance of considering the spatial and temporal heterogeneity of agricultural landscapes when assessing the population dynamics of nontarget arthropods in the context of the risk from the use of plant protection products. A need is identified to further develop and thoroughly validate predictive population models, which can incorporate all factors relevant to a specific system. Once reliable predictive models for a number of representative nontarget arthropod species are available, they could provide a meaningful tool for refined risk evaluations (higher tier level risk assessment), addressing specific concerns identified at the initial evaluation stages (lower tier level risk assessment). *Environ Toxicol Chem* 2021;40:2667–2679. © 2021 ERM, FMC, Syngenta, Bayer AG, BASF SE, Corteva agriscience. *Environmental Toxicology and Chemistry* published by Wiley Periodicals LLC on behalf of SETAC.

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INTRODUCTION

The influence of environmental heterogeneity of habitats in space and time on local population dynamics has long been recognized, as have the mechanisms leading to different

demographic parameters (mortality, reproduction, immigration, emigration). These mechanisms are directly linked to the dynamics of colonization, extinction, and recolonization of habitat patches, in many cases leading to an assemblage of local (sub)populations that are connected by migration—a so-called metapopulation (MacArthur and Wilson 1967; Levins 1969; Hanski and Gyllenberg 1993). Numerous metapopulation models have been described relying on different assumptions of the distribution of habitat patch size and the level of dispersal of subpopulations within the landscape (see Levins 1969; Hanski 1998). Classically, a continuum of environmental conditions are described ranging from isolated/fragmented habitat patches with little dispersal among the

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subpopulations, leading to high genetic differentiation, to closely connected habitat patches with high dispersal ability and thus gene flow leading to little or no genetic differentiation between subpopulations (Harrison and Taylor 1997; Cheptou et al. 2017). Knowledge of the life-history characteristics of the species and the demography, dispersal, and genetic variance of subpopulations in a specific landscape is essential to define the appropriate spatial (and temporal) scale at which metapopulation dynamics should be investigated (Harrison and Taylor 1997; Hanski et al. 2011).

The concept of source-sink dynamics was first described in the mid-1980s by Holt (1984, 1985) in the context of predator–prey dynamics and was further developed by Pulliam (1988). It considers that in many landscapes, populations inhabit habitats of varying quality where some patches have a deterministic extinction without immigration. The concept of Pulliam (1988), subsequently considered the “classical” source-sink concept, is that a significant proportion of many populations may occur in lower quality “sink” habitats where the within-habitat reproduction is insufficient to balance local mortality but that in these sink habitats, populations could persist if they were maintained by immigration from more productive “source” habitats. On this basis, an equilibrium can be maintained in each habitat by a balance of 4 key demographic parameters: mortality, reproduction, immigration, and emigration. This source-sink concept views populations from a “metapopulation” perspective, that is, one in which a population is made up of a number of local, semi-autonomous subpopulations linked to each other by dispersal (Gilpin and Hanski 1991).

Since this description of the classical source-sink concept by Pulliam (1988), a number of articles were published in the late 1990s and early 2000s addressing some aspect of source-sink dynamics (see Runge et al. 2006 for a quantitative assessment of the available literature on this topic). Successive theoretical subconcepts based on case-specific modifications of the classical source-sink concept have been introduced, such as pseudo-sink attractive sink and ecological trap (Delibes et al. 2001; Donovan and Thompson 2001; Robertson and Hutto 2006). Other authors partially overlap metapopulation concepts like ecological trap or action at a distance with the source-sink concept (Spromberg et al. 1998; Schlaepfer et al. 2002). Many of the articles have been of a theoretical nature, and a review by Diffendorfer (1998) found that there were relatively few empirical studies to support different population models (including source-sink). More recently, a review of Heinrichs et al. (2019) concluded that the proportion of studies based on empirical data was approximately the same or slightly higher than modeling studies, although modeling studies that relied heavily on empirical data were considered as empirical studies. Heinrichs et al. (2019) also found that the majority of publications addressing source-sink dynamics explicitly studied mammals, birds, and aquatic invertebrates and focused mainly on forested habitat and conservation aspects. Only a limited number of studies investigated source-sink dynamics in agricultural habitats or used terrestrial invertebrates.

In 2015 the source-sink concept appeared for the first time in the regulatory context of European risk assessment of plant protection products for nontarget organisms. The European Food Safety Authority (EFSA), an agency funded by the European Union that has (scientific) responsibility for risk assessment in relation to food safety, published a Scientific Opinion addressing the state of the science on risk assessment of plant protection products for nontarget arthropods (European Food Safety Authority 2015). This Scientific Opinion presented a proposal on how predictive simulation modeling may be used to assess the potential risk of indirect effects of long-term pesticide application in agricultural fields on off-field populations due to source-sink dynamics in a landscape-level risk assessment approach. Whereas this is an important development in the use of population modeling in environmental risk assessment for nontarget arthropods, we identified the need for a more exhaustive review of the theoretical concepts addressing source-sink dynamics as well as their applicability for arthropods in agro-ecological systems. Specifically, the objectives of our review were 1) to provide an overview of the published theoretical concepts and definitions of source-sink dynamics and review the empirical evidence for these theoretical concepts, to put into context the landscape-level risk assessment approach presented in the EFSA Scientific Opinion; 2) to discuss the applicability of the existing source-sink concepts for the prediction of population dynamics of arthropods in agro-ecological systems and identify potential limitations; and 3) to discuss the way in which source-sink dynamics could be implemented within a regulatory framework of environmental risk assessments.

METHOD OF LITERATURE REVIEW

The present review considered published studies related to theoretical concepts and definitions of source-sink dynamics and assessed the empirical evidence of source-sink dynamics obtained from experimental systems and field observations. The focus was on arthropods in agricultural systems, although other examples were included if they were considered relevant to facilitate the understanding of specific source-sink concepts for which no or only limited examples for arthropods were available. Relevant databases were searched (PubMed, SciDir, and STN), and a number of search terms were considered, using relevant linkages, relating to source-sink (including ecological trap), “action at a distance,” populations (including habitat, metapopulation, and dynamics), arthropods/insects, and agriculture (including farmland and crops). Studies considered were those published from 1986 onward, to take into account the period relating specifically to the consideration of source-sink effects. The selection of relevant studies was based on providing a good overview of the theoretical concepts and a complete selection of the available empirical evidence for source-sink dynamics in relation to arthropods in agricultural systems that were identified with our search terms and via cross-references from the studies identified. (The references reviewed are listed in the Supplemental Data, S1).

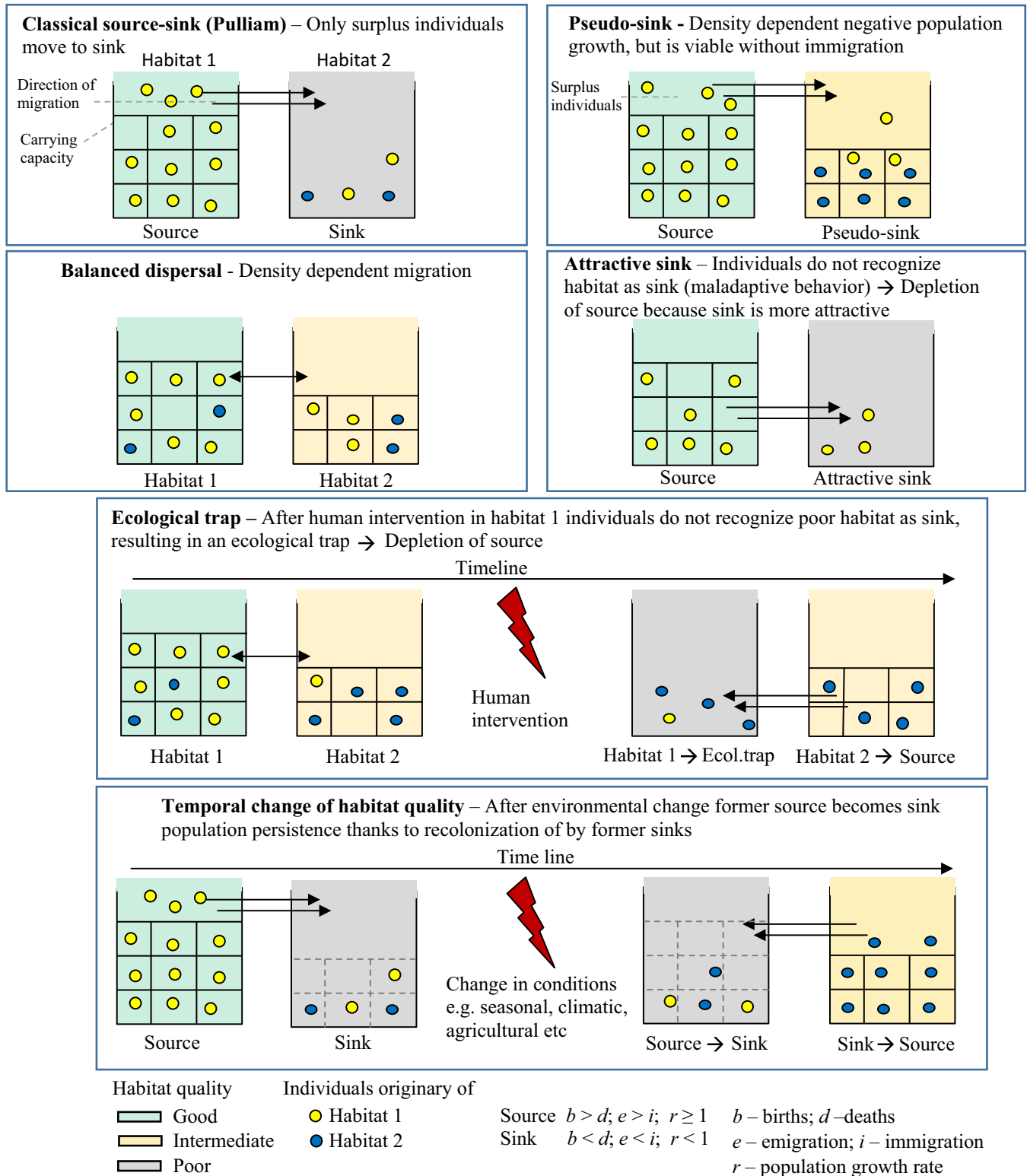


FIGURE 1: Representative theoretical population models related to source-sink dynamics.

THE SOURCE-SINK CONCEPT

Theoretical approach

There is a considerable body of research addressing the theoretical aspects of source-sink dynamics. The first objective

of the present review was to provide an overview of the most prominent source-sink concepts described in the literature (classical source-sink, pseudo-sink, attractive-sink, and ecological trap; see Figure 1 for an illustration). During the review, it became clear that in many cases definitions and the use of

concepts are not consistent across authors and that the use and definition of terms has changed over the years, which can lead to some confusion. We tried to be as complete and transparent as possible. Further source-sink population models considering temporal variability (disturbance) of habitats, a relevant factor in agricultural landscapes, are presented, including the source-sink model used in the EFSA Scientific Opinion of nontarget arthropods (European Food Safety Authority 2015).

Classical source-sink concept

The first appearance of the term “source-sink dynamics” dates from a publication of Holt (1984, 1985), which was further developed by Pulliam (1988), who proposed that a proportionately large part of a population could occur in low-quality sink habitats, where within-habitat reproduction is not sufficient to balance local mortality. However, it was considered that populations could persist in such habitats as a result of continued immigration from more productive good-quality source areas nearby. A definition based on this concept is given in Dias (1996): “For a given species, good quality habitats yield a demographic excess (natality > mortality), while lower quality habitats yield a demographic deficit (mortality > natality) and may not persist without immigration from sources. The demographic dynamics are balanced in each habitat, and in the whole population, by dispersal, with net emigration from the source and net immigration into the sink.” The sink populations are thus being maintained by the surplus from sources, with the assumption that animals dispersing actively are able to recognize less favorable sink habitats and avoid them unless no better alternatives are available. This can result in an ecologically and evolutionary stable state, with both source and sink habitats occupied (Pulliam 1988). In reality, sufficient stability to allow such an equilibrium state to develop may not occur in many landscapes such as farmland, where there are regular disturbances related to land cultivation. This means that conditions for natality, mortality, and migration are likely to change abruptly over time, thus altering the outcome of the metapopulation dynamics.

Pseudo-sink

Pseudo-sink populations are defined as populations that may appear to be nonviable simply because the dispersal of individuals into them depresses fecundity or increases mortality as a result of density-dependence (temporary negative population growth), whereas in fact the populations are viable without immigration but on a lower carrying capacity level (Watkinson and Sutherland 1995). Although the authors acknowledged that sinks can and do occur, they concluded that it is almost impossible to identify sources and sinks simply by demographic measures of the birth and death rates operating within populations.

Attractive sink

Whereas classical source-sink theory assumes that dispersing animals have an active role in terms of the migratory choices (i.e., they can recognize and, when possible, avoid

low-quality [sink] habitats and select source habitats first), this is not the case in attractive sinks. An attractive sink results from maladaptive behavior, with sinks being erroneously identified as favorable habitats, that is, they are perceived as good source habitats (Delibes et al. 2001). In this case, it is the decision-making process of individuals to preferentially settle in sink habitats that influences the dispersal rates. The consequence of poor habitat selection is that the sink habitats take on greater significance within the metapopulation and tend to lose any positive role they may have (see the later section, *Source-sink population models considering temporally variable habitats*), with the result that the whole metapopulation may start to decline. Delibes et al. (2001) used a simple deterministic model with which they demonstrated the importance of identifying species' habitat preferences as well as the proportion and demographic parameters of different habitat types, to obtain reliable conclusions about measured population trends.

Ecological trap

The term ecological trap has been used to describe a habitat that is “low in quality for reproduction or survival and cannot sustain a population, yet it is preferred over other available, higher quality habitats” (Donovan and Thompson 2001). It is considered that ecological traps may occur as a result of sudden environmental change resulting in the cues that individuals use to assess habitat quality becoming “uncoupled” from the true quality of the environment (Shochat et al. 2005; Robertson and Hutto 2006). This situation arises particularly as a result of human disturbance, and this aspect differentiates ecological traps from attractive sinks, where there is poor recognition of habitat quality. In the case of ecological traps, habitat changes occur relatively quickly such that organisms are not able to recognize the relevant cues (i.e., they continue to use the original ones) and so are not able to adapt to the changes quickly enough. Based on the original definition, not every ecological trap might be considered as part of source-sink dynamics, because this is very much dependent on the level and direction of dispersal between the subpopulations (Schlaepfer et al. 2002). Traps could also be subpopulations with suddenly reduced fitness but individuals are not emigrating, although higher quality habitats would be available in the surroundings.

In more recent years, Battin (2004) proposed a graphical representation of the relationships among sources, sinks, and traps based on the combinations of habitat selection and habitat quality, in which traps are the specific combination where low habitat quality is actively selected, thus rather considering the ecological trap as a specific type of sink population. Thus the distinction between attractive sinks and ecological traps may not always be clear, depending on the identification of the relevant aspects of habitat quality and selection; individual dispersal ecological traps could be seen as a subset of or even a synonym for attractive sinks (Battin 2004). It should also be noted that density may not always be positively correlated with habitat quality (Van Horne 1983), and therefore Pärt et al. (2007) proposed a protocol for

investigating ecological traps at the individual level by linking the cues used for habitat selection to fitness.

Hale et al. (2015) concluded there was mounting evidence (based on metapopulation modeling) that ecological traps are likely to become increasingly common as a result of human impact. Pärt et al. (2007), on the other hand, considered that the empirical evidence for the existence of ecological traps is lacking and that no study showed evidence of an ecological trap in its strict sense (i.e., a preference for sink and avoidance of source habitats). However, this was based primarily on a consideration of birds; a few potential examples of ecological traps involving insects are presented in the later section, *Empirical Evidence: Experimental Systems and Field Studies*.

Source-sink population models considering temporally variable habitats

Most of the theoretical source-sink concepts assume stability of habitat quality, which in real-world situations is rarely the case. In particular, the agricultural landscape is characterized by a series of seasonal disturbances such as harvest, tillage, pesticide applications, and other cultivation measures. Any field management activity can have a direct impact on mortality and natality of species living there, but it can also alter the attractiveness of the field and thus may influence migration dynamics.

A number of theoretical considerations can be applied to an unstable environment and its impact on source-sink dynamics. When the environmental conditions in a habitat are not constant but fluctuate, the quality of a source habitat may become temporarily worse than a connected permanent sink habitat (Frouz and Kindlmann 2015). Similarly, a cycle of disturbance and subsequent recovery could result in a patch alternating between serving as a source and a sink (Falcy and Danielson 2011). In these cases, allocating offspring to sink habitats may increase the reproductive success of an individual and potentially result in an increased likelihood of metapopulation growth and persistence. It has also been suggested that populations could possibly persist in variable environments that only consist of sink habitats (Jansen and Yoshimura 1998). Clearly this is important in the context of the agricultural environment, where crops could provide both sources and sinks either spatially (given crop heterogeneity) and/or temporally (with seasonal changes).

A theoretical modeling approach attempting to identify factors that affect the strength of source-sink dynamics concluded that overall a diverse combination of factors is relevant and that simple inference of process from pattern is likely to be inappropriate to assess and predict source-sink dynamics (Heinrichs et al. 2016). As an example, Halley et al. (1996) demonstrated with a complex model of arthropod dispersal (based on a linyphiid spider) in an agricultural environment the importance of landscape heterogeneity for survival and abundance. Small changes in the ratio of source and sink habitats, in this case grassland in large areas of cereal production, dramatically increased spider populations. Furthermore, the inclusion of low-quality habitats (areas hostile to spiders, with

high mortality, referred to as “nonhabitat areas”) in the landscape could provide temporary refugia in landscapes with heavy pesticide use. Furthermore, the model showed that temporal correlation of insecticide application (all fields sprayed the same day) as well as spatial correlation (all arable fields in the landscape of the same type) sharply increased the negative effects on the spider population.

Source-sink dynamics in the context of environmental risk assessments

Metapopulation processes such as source-sink dynamics have also been discussed in the context of risk evaluation of plant protection products; the importance of such dynamics in assessing the long-term risk of pesticides to nontarget arthropod populations at the landscape level has been raised (Sherratt and Jepson 1993; Topping et al. 2014, 2015). Another concept in this context is that of “action at a distance,” which describes a system of interconnected habitat patches, in which noncontaminated subpopulations can be impacted indirectly by the mortality in a toxicant-exposed subpopulation via alteration in the dispersal from this contaminated subpopulation and without direct exposure to the contaminant (Spromberg et al. 1998). Whether the action at a distance is corresponding to a source-sink dynamic will ultimately depend on how the alteration of dispersal will take place, which role the affected subpopulation has in terms of emigration to other subpopulations, and whether or not the metapopulation will adapt the habitat selection following the habitat disturbance (i.e., will there be an adaptive or maladaptive behavior to the new situation).

The EFSA Scientific Opinion addressing the state of the science on risk assessment of plant protection products for nontarget arthropods (European Food Safety Authority 2015) introduces the source-sink concept into the regulatory context for Europe. It presents a proposal for how source-sink models evaluating potential indirect effects from long-term in-field pesticide exposure on off-field populations at the landscape level may be developed for regulatory purposes. The classical source-sink concept of Pulliam (1988) is cited in the EFSA Scientific Opinion (European Food Safety Authority 2015) and is used synonymously with action at a distance. Although there are some similarities between the concepts, we would like to highlight relevant differences. The action at a distance model of Spromberg et al. (1998) is a general concept, describing the situation in which “mortality in one subpopulation has ecologically significant effects on non-dosed subpopulations.” Pulliam (1988) defines source-sink dynamics as the result of active dispersal in environments with heterogeneous habitat quality (i.e., active habitat selection). Simply put, populations in less preferred sink habitats are maintained by surplus individuals migrating across from highly attractive, more productive source habitats. Therefore, as just mentioned, in some situations action at a distance could be considered as source-sink, and in others not, depending on the dispersal of the affected subpopulation in the metapopulation network and the habitat preference of the individuals.

In the EFSA Scientific Opinion, a specific example is given of how source-sink dynamics might be important in consideration of a predictive model based on a case study of the carabid beetle, *Bembidion lampros* (Bilde and Topping 2004; Topping et al. 2015). The objective of this model was to assess the potential of long-term in-field pesticide application (over 30 yr) to have effects on unexposed off-field populations, assuming the involvement of source-sink dynamics. The life cycle for *B. lampros* involves adults emerging in autumn, overwintering in vegetated field boundaries, and then dispersing during spring into arable fields, where they reproduce and then die (Petersen 1999). Optimal breeding habitats are modeled as agricultural fields, whereas some limited off-field landscape elements are considered as a suitable but suboptimal breeding habitat. All agricultural fields in the landscape were exclusively cultivated with the same crop, and insecticide application was applied synchronously (the same day) in the whole landscape and during the breeding activity of adult beetles. The authors concluded that 1) clear off-field effects from in-field mortality was observed, 2) there was a clear impact of long-term year-on-year application of pesticide, and 3) landscape structure clearly influenced the results (European Food Safety Authority 2015; Topping et al. 2015).

EMPIRICAL EVIDENCE: EXPERIMENTAL SYSTEMS AND FIELD STUDIES

We reviewed publications that have assessed how the different theoretical source-sink concepts are manifested in experimental systems or in field studies. This aspect focused on arthropods in agricultural landscapes. However, relatively few empirical studies investigating source-sink dynamics of arthropods in agricultural landscapes were identified, and so studies addressing arthropods or agricultural landscapes only were also assessed. Other examples were included if they were considered helpful for the understanding of a particular concept.

Experiments and field observations indicating classical source-sink

A laboratory experiment was conducted with clonal metapopulations of *Daphnia magna* reared in systems with different levels of fragmentation and patch quality (Drake and Griffen 2013). The results showed that population persistence was maximized at intermediate levels of habitat fragmentation. The authors also showed that a source-sink population structure decreased average metapopulation size and increased its variability compared with populations in which resources were evenly distributed between habitat patches. Both habitat fragmentation and resource concentration therefore had implications for the risk of extinction (Drake and Griffen 2013). This may be relevant for the agricultural environment, where differing levels of heterogeneity and resource distribution are found, although it is not clear whether the simplistic laboratory model applies to this real-world complexity because some source-sink models indicate increased persistence at the metapopulation level. In another laboratory study, using protist

microcosms as a model system in combination with mathematical modeling, it was concluded that dispersal not only redistributes competitors but can also alter demographic rates, for example, as a result of resource extinction or movement of nutrients by dispersers (Fox 2007). This suggests that although source-sink dynamics can affect competitive outcomes due to the movement of individuals, there may be other factors involved, which also need to be taken into consideration.

Moving into the field, an investigation of carabid beetle populations in an agricultural environment showed that in spring, the landscape composition and configuration of annual crops and noncrop habitats greatly influenced carabid activity-density observed in crop fields (Duflot et al. 2016). It was considered that these dynamics result from the seasonality of crop fields, which could generate habitat complementation and source-sink processes (i.e., spatial redistribution of species over time). However, the conclusions were based on activity-density only (community composition at different time points based on pitfall trap data) and did not involve any measurement of the 4 key demographic parameters (the rates for birth, death, emigration, and immigration). Another field experiment carried out on planthoppers (*Prokelisia crocea*) and egg parasitoids (*Anagras columbi*) did investigate the effects of immigration and emigration together with landscape structure on the source-sink dynamics of fragmented populations (Cronin 2007). It was concluded that increased habitat fragmentation and emigration losses are likely to destabilize regional population dynamics. This has implications for the agricultural environment, where habitat fragmentation is dependent on the field structure and cropping pattern and losses due to emigration and mortality will be influenced by agricultural activities including pesticide application.

Experiments and field observations indicating ecological traps or attractive sinks

Although a number of examples of ecological traps that involve passerine birds breeding in North American woodlands have been identified (Gilroy and Sutherland 2007), these habitats are not comparable to the relatively rapid change in habitat conditions that can occur in the agricultural environment (as a result of seasonal and cultivation factors) such that favorable conditions could be changed to unfavorable ones within the life cycle of an organism.

Experimental studies of habitat selection in dragonflies, damselflies, and mayflies have demonstrated the potential for ecological traps occurring in insects. Orientation to polarized sources of light is an important mechanism that these insects use in their search for a suitable site for oviposition. Thus, some types of asphalt also polarize light with the result that they can be attractive to mayflies for oviposition, leading to detrimental effects on reproduction success (Kriska et al. 1998), and similarly, crude oil slicks may be attractive oviposition sites for dragonflies (Horváth and Zeil 1996). Another potential example of ecological traps involving insects is found in the study of Ries and Fagan (2003) with the mantid *Stagmomantis limbata*. They examined oviposition preference, predation, and parasitism rates at 2 forest edge types (cottonwood and desert scrub) in

comparison with interior habitat (nonedge). It was concluded that in this case an ecological trap may exist because both oviposition density and bird predation rate of oothecae was increased at forest edges (more consistently at desert scrub edges). Similarly, Konvicka et al. (2006) found that the butterfly *Parnassius mnemosyne* did not recognize the unsuitability of a farmland biotope in comparison with the more favorable woodland habitat.

An experimental study on root vole populations (Gundersen et al. 2001) aimed to examine some of the critical assumptions often made in source-sink models including those involving ecological traps. Comparison of demographic parameters was made in a 2-patch system with high mortality patches (sink populations) being simulated by pulsed removal of animals while in the other patches no animals were removed (source populations). In the presence of this simulated mortality, an increased emigration rate from source patches led to them having a negative population growth such that they actually became sinks. In this experiment habitat, quality cues, which would allow individuals to recognize low-quality habitats, were missing (the sinks were created by artificial removal of animals from the patches), but they are effectively simulating an ecological trap or an attractive sink.

Temporal inversion of source and sink habitats

As mentioned earlier, theoretical source-sink concepts assume stability of habitat quality, but in reality, this is not often the case and the role of different areas in metapopulation dynamics can change over time. A temporal change of pseudo-sink to source and from source to sink populations was observed by Thomas et al. (1996), who were investigating a metapopulation of the checkerspot butterfly. Source population in clear-cut patches of forest became extinct after a severe summer frost that killed the host plants. Populations in outcrop areas declined but still persisted, indicating that they were pseudo-sinks. Subsequent experiments demonstrated that the relationship between the populations in the different habitats had changed after the extinction of the sources due to the frost (Boughton 1999). Recolonization of the clearings from the outcrop areas occurred. However, the recolonization rate was relatively low due to the poor reproductive success of immigrants (in comparison with resident populations where they became established in clear-cut areas). The overall consequence of this was that the net flow of the butterflies had changed after the frost, with the pseudo-sinks becoming sources while the clearing populations had become sinks. As a result of the change in the local conditions, the butterfly metapopulation had undergone a source-sink inversion from one locally stable state to the other.

The importance of taking into account the temporal variation in source-sink dynamics by setting an appropriate time scale when investigating metapopulation dynamics has been shown by Johnson (2004) in a study on the herbivorous neotropical rolled-leaf beetle *Cephaloleia fenestrata* (Chrysomelidae) in upland and flood zone areas in Costa Rica. Whereas the system lacked source-sink dynamics during non-flood periods, this situation changed after flooding, which

greatly decreased survival in the flood zone areas. As a result, migration became directional from the upland to the flood zone habitat, which had thus become a sink. In the agricultural environment, ploughing, harvest/mowing, or pesticide application could be the equivalent of flooding in this system. Clearly, the frequency of changes in a source-sink system will depend on the pattern of any disruption. In the case of the agricultural environment, the disturbances related to land cultivation are generally of a cyclic nature with consequences for the metapopulation dynamics. Climatic extremes can be another form of disturbance. For example, Frouz and Kindlmann (2001) investigated the source-sink relationships in terrestrial chironomids that specialize in open patches in initial stages of succession or in open, disturbed areas (such as arable land), and so these can be considered as source habitats. However, these areas are also prone to summer desiccation, resulting in marked reductions in the larval generation or even resulting in local extinction. Recolonization subsequently occurs in the winter from less suitable but more stable sink habitats in the surrounding environment. It can be concluded that source habitats can maintain populations in the sink habitats, which in turn can quickly colonize the seasonally dependent source habitats, thus maintaining overall persistence. Although the sink habitats are more stable, they are not favorable for reproduction and require immigration from source habitats to be maintained over time.

Different population dynamic concepts in the same system

There are other population models, in addition to source-sink, that may be relevant depending on the circumstances. For example, balanced dispersal assumes that populations are regulated in a purely density-dependent fashion and that although habitats may vary in quality (carrying capacity), there are no sinks (McPeck and Holt 1992; Lemel et al. 1997). Balanced dispersal also assumes that there are no constraints on dispersal (no net flow of movement) and that fitness becomes equal across all habitats (Diffendorfer 1998). As a general rule, it is considered that species with high vagility and the ability to assess habitat quality should tend toward balanced dispersal, whereas at the other end of this continuum, source-sink dynamics will be more common (Diffendorfer 1998). A few studies investigated metapopulations with the specific objective to identify whether the (meta)population dynamics followed a source-sink or rather a balanced dispersal model. Comparison of emergence and recruitment in a metapopulation of the mayfly *Callibaetis ferrugineus hageni* (Baetidae) revealed that some ponds in the observed system were net exporters of females and others were net importers (Caudill 2003). Overall, the data were more consistent with a source-sink dynamic than with balanced dispersal because patches differed in quality, and because there was a corresponding net migration of individuals between them (i.e., from sources to sinks). The results thus support the hypothesis that local and regional population dynamics are influenced by spatial variation in patch quality, and by the ability of individuals to disperse among them and to assess their quality. However, to assess whether this was

actively directed migration, reflecting source-sink dynamics, rather than just driven by density, it would be necessary to identify the cues being used to assess habitat quality.

Another study compared the classical source-sink and balanced dispersal models in populations of the wood mouse in arable farmland (Tattersall et al. 2004). In this case, it was concluded that in general, the balanced dispersal model described wood mouse populations better than the source-sink model, although the authors also noted that more than one model for dispersal dynamics may apply within the same landscape. Thus, in-crop dynamics at one site was hypothesized to be an attractive sink on the basis that survival there was particularly low, which was attributed to indirectly assessed cultivation measures (farming costs for pesticides and fertilizers).

The complexity of metapopulation dynamics is also highlighted in a study that investigated the population dynamics of a solitary bee species (*Andrena humilis*) involving large alternate-year population fluctuations (Franzen and Nilsson 2013). Although this may have been the result of source-sink dynamics, a number of other mechanisms were also considered, for example, prolonged diapause responding to unpredictable disturbances in the weather or resource availability or a bet-hedging strategy to avoid natural enemies and allow survival in small habitat patches that are important for metapopulation persistence. This shows that long-term studies may be needed to identify the important factors influencing the population dynamics.

This complexity also applies to spatial heterogeneity; a study looking at the valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*) in California (Talley 2007) provides an example. That study showed that the beetle's population has predominantly a patch-dynamic structure but that other processes are involved reflecting all forms of heterogeneity (patch, gradient, and hierarchy). Thus, as well as considering the relevant time scale, it is also necessary to ensure that the appropriate spatial scale, encompassing the relevant landscape heterogeneity, is taken into account when considering the mechanisms that may be involved at the metapopulation level. The spatial scale at which this heterogeneity needs to be considered can also vary. Thus, biotic and abiotic factors may vary within a continuous environment such that population outcomes vary in different habitat patches. In a study on the crane fly, *Tipula paludosa*, a source-sink dynamic system was identified at either end of a gradient of the distribution of low- and high-quality habitat patches (linked to low and high soil moisture level; Petersen et al. 2013). However, in an intermediate zone where the patch quality became more variable, this dynamic was less evident and the occurrence of suitable but sparsely populated habitats tended to increase. This indicates that metapopulation dynamics and source-sink mechanisms may depend on the spatial distribution of habitat patches with different qualities.

The potential importance of spatial scale when assessing population level effects is also shown in a study looking at predatory lacewings (*Chrysoperla* spp.) in cotton fields (Roseenheim 2001). Spatial heterogeneity in aphid prey densities interacted with the intensity of higher order predation of

lacewing larvae and so appeared to produce source-sink dynamics. Thus, higher order predators could result in a decline in *Chrysoperla* densities when migration was prevented but the magnitude of this effect was influenced by aphid densities (higher larval survival with higher aphid densities). The results indicated the existence of sinks or pseudo-sinks. However, the study was conducted in small caged and uncaged plots within larger unbroken plantings, so immigration in the latter case may well have come from nonexperimental areas. Although there were indications that the caged populations could decline to a lower but stable density, which could mean that the cotton fields were operating as pseudo-sinks, it would be necessary to consider populations at the field level to assess this at a relevant spatial scale. Indeed, it is important when assessing any field data to consider the spatial scale over which it has been generated to see whether there are any implications at the metapopulation level.

DISCUSSION

Source-sink dynamics

Since the description of the classical source-sink concept by Pulliam (1988), a considerable body of research has been published addressing the theoretical aspects of source-sink dynamics. We have reviewed a selection of the most prominent theoretical models, which are illustrated in Figure 1. However, although these theoretical models are designed for hypothesis formulation and testing, they are of limited use in terms of predicting effects on population dynamics. This is reflected in the restricted number of publications that have been identified showing empirical evidence for source-sink dynamics. Similarly, the reviews of Runge et al. (2006), Furrer and Pasinelli (2016), and Heinrichs et al. (2019) identified that in-depth assessments of the source-sink status of populations based on an equal consideration of all 4 relevant demographic parameters (death, birth, emigration, and immigration) are scarce. The most recent review of studies using source-sink dynamics, by Heinrichs et al. (2019), classified the studies as “empirical” if they focused on collecting or analyzing field data (including modeling studies relying heavily on empirical data), as “experimental” if they physically manipulated a field system or microcosm, and as “modeling” if the studies did not collect or rely on empirical data. This classification differs from the one used in the present review, where we have considered studies as empirical if the assessment of source-sink dynamics was based on field observations or experimental set-ups, whereas modeling studies, even when the biological model relied on empirical data, were considered as a more theoretical approach.

Heinrichs et al. (2019) found that the proportion of studies based on empirical data was approximately the same or slightly higher than that of modeling studies, whereas there were very few experimental publications. Importantly though, it was reported that whereas 79% of studies based on empirical datasets claimed to identify source-sink dynamics, only 13% of these studies based their assessment on all 4 key demographic measures (reproduction, mortality, immigration, and emigration), and nearly 23% used neither demographic nor

movement metrics to make conclusions about the presence of source-sink dynamics. Furthermore, the review of Heinrichs et al. (2019) found that the majority of studies with empirical evidence focused on birds, mammals, and forested systems. This agrees with our review, which identified very few empirical examples in which a source-sink mechanism had been identified for nontarget arthropods in an agricultural environment (see Rosenheim 2001; Petersen et al. 2013). The study of Dufлот et al. (2016) concluded similarly, although their source-sink evaluation was based only on activity-density (pitfall trapping) and did not explicitly assess the 4 demographic parameters relevant for source-sink dynamics.

There is also little agreement on which parameters are relevant for the strength of observed source-sink dynamics. Caudill (2003) hypothesized that the ability of individuals to disperse and to assess the quality of habitat patches tended to favor source-sink dynamics. The authors of the EFSA Scientific Opinion (European Food Safety Authority 2015) considered source-sink to be especially relevant for highly mobile species with population ranges larger than field size, and they did not consider the species' ability to assess habitat quality. From this perspective, they concluded that there was a need to assess the impacts of source-sink dynamics on the landscape scale (beyond treated fields). Heinrichs et al. (2016) concluded on the basis of a modeling approach that dispersal ability had a relatively weak impact on the strength of source-sink dynamics, and moreover, that long-distance dispersers rather tended toward weaker source-sink systems, which contrasts with the assumptions made in the EFSA Scientific Opinion (European Food Safety Authority 2015). Similarly, Frouz and Kindlmann (2015) hypothesized that the beneficial effects of permanent (sink) habitats on metapopulation persistence were found to be reduced when the species dispersal ability was high and when environmental conditions (e.g., seasonal changes leading to population depletion) were not synchronized, whereas sink habitats were particularly important for metapopulation persistence when species only dispersed over short distances (low dispersal ability) and conditions were synchronized. The finding of source-sink like dynamics in the EFSA Scientific Opinion (European Food Safety Authority 2015) example is potentially explained by the high degree of synchronization (all fields with same crop, treated the same day, for 30 yr). It would be interesting to see the effect on the model outcome if a realistic crop-rotation scenario or a certain level of temporal and spatial stochasticity in the insecticide application is assumed, to assess the sensitivity of the model outcome.

Application to the agricultural environment

The characteristics of the agricultural landscape, which is composed of spatially and temporally variable habitats, need to be taken into account when evaluating potential source-sink dynamics in agro-ecological systems. The concept of Pulliam (1988) assumed that source and sink habitats are temporally and spatially fixed, that is, that the populations are in equilibrium. Further studies that have taken into account temporal dynamics indicate that the relationship between sources and

sinks can significantly change over time (see Boughton 1999; Frouz and Kindlmann 2001; Falcy and Danielson 2011). In this context sinks can indeed provide stability (resilience and persistence) for a metapopulation rather than being only a sub-optimal habitat for surplus individuals from a source or even a drain on the source populations. This indicates that spatial and temporal heterogeneity could benefit biodiversity and enhance local and regional population persistence in agricultural landscapes (Vasseur et al. 2013; Villemey et al. 2015).

In the agricultural landscape, cyclic disturbances related to land cultivation such as ploughing, planting (considering crop rotation), harvesting, and pest management (control of pest insects, diseases, and weeds) over the growing season keep most agricultural fields in early succession states. Agro-ecological systems are thus a product of prolonged human activity and as a result, they tend to contain eurytopic species, which are able to deal with the temporal and spatial heterogeneity of agricultural habitats (Thiele 1977). In these systems it is possible that both in-field and off-field habitats maintain temporal source populations. Standard agricultural operations can directly affect mortality (Rowen et al. 2020) and emigration rates, potentially turning a source into a sink population (Thorbeck and Bilde 2004).

Crop harvest, mowing, and ploughing largely destroy these habitats and force migration of soil- and leaf-dwelling species to areas that are still vegetated. In turn, replanting and cultivation usually re-create new temporal habitats, that will be repopulated from other cropped fields or the off-field environment. This will modulate dispersal, so that initial attraction for a treated plot may increase an action at a distance (acting as an ecological trap), and subsequently a lack of attraction or even repellence (e.g., due to low food availability) may weaken action at a distance. Temporal and spatial heterogeneity are generally linked, because different crops require cultivation management at different times during their cropping cycle. In addition, from a farmer's perspective, crop diversification can also contribute to economic resilience by spreading both agronomic and market risks (Barzman et al. 2015; Struik and Kuyper 2017).

The crucial importance of landscape composition and configuration as well as the temporal and spatial synchronization of disturbances (e.g., agricultural operations) on metapopulation dynamics has been highlighted in a model for linyphiid spiders (Halley et al. 1996). Similarly, an individual-based simulation model on linyphiid spiders showed that landscape diversity and temporal heterogeneity are crucial for the persistence of spiders in the agricultural landscape (Thorbeck and Bilde 2004). These findings are in agreement with the conclusion from studies based on field evidence in temporal and/or spatial heterogeneous systems, that population dynamics can often not be described by one specific metapopulation concept, such as source-sink, alone (Tattersall et al. 2004; Talley 2007; Franzen and Nilsson 2013).

The predictive simulation model for *B. lampros* of Topping et al. (2015) assumes a landscape with a monoculture of winter wheat and highly synchronized pesticide application over a time period of 30 yr. The model predicts an optimal

reproduction habitat for this species within agricultural fields, which the model assumes to occur during pesticide application (assuming 80% mortality). The species is further characterized by bi-annual migration between field boundaries and in-field habitat. Given these model parameters, the observed outcome of a reduction in off-field populations due to in-field exposure to pesticides does not seem surprising. Because most reproduction takes place in the agricultural field, the in-field population could thus be considered as a source. *Bembidion lampros* does not overwinter in-field and an important seasonal migration to the off-field takes place, therefore the off-field could be considered as a sink population (with no or low reproduction and maintained only by immigration). Alternatively, if the off-field provided a permanent habitat with a low carrying capacity during the breeding season, then it could be a pseudo-sink. The role of the off-field population in the metapopulation dynamic is relevant; it raises the question of whether the model is able to identify true off-field impacts, because seasonal migration of in-field populations to off-field occurs. In this case, the *B. lampros* metapopulation is primarily driven by in-field effects, which translate to off-field due to migration. These effects are potentially already addressed by consideration of the standard in-field risk assessment alone. Another relevant question is directed to the metapopulation status of the in-field and off-field populations. If the in-field and off-field are considered to accommodate one population, then the source-sink concept should be enlarged to surrounding landscapes. The widely distributed and eurytopic species *B. lampros* could serve as a suitable surrogate species for such an adapted model.

In addition, it has been highlighted in several studies that a narrow view of the system, such as a focus on the wrong spatial scales or an inappropriate type of heterogeneity, can lead to the wrong conclusions (Halley et al. 1996; Tattersall et al. 2004; Thorbek and Topping 2005; Talley 2007; Franzen and Nilsson 2013). It would therefore be useful to understand the sensitivity of the model parameters related to the diversity of cultivated crops (30 yr of monoculture vs crop rotation), and a realistic degree of asynchrony of pesticide application, on the outcome of the population model. The impact of these cultivation parameters is also relevant in the light of implementing integrated crop management and other measures of the Sustainable Use Directive of the European Commission (2009a), according to which crop rotation and integrated pest management have been mandatory since 2014.

Implementation into risk assessment schemes

The proposal in the EFSA Scientific Opinion (European Food Safety Authority 2015) for consideration of metapopulation dynamics of nontarget arthropods in the European regulatory risk assessment for the use of plant protection products does raise important questions about the relevance of spatial and temporal scales. However, in this context it is important to differentiate between the evaluation of landscape intrinsic effects and effects caused by the intrinsic toxicity of plant protection products on arthropod metapopulations. The purpose

of the risk assessment according to the European plant protection product regulation (European Commission 2009b) is to assess whether the use of a product in compliance with the principles of Good Agricultural Practice will have the potential of unacceptable effects on nontarget organisms. Although it is acknowledged that the landscape is important for metapopulation dynamics, the plant protection product risk assessment is not laid out to evaluate the potential quality of the landscape for nontarget organisms nor to influence the way agriculture is conducted. It is important to realize that decisions regarding the transformation of the agricultural landscape or agricultural systems are not part of the risk assessment because such decisions highly depend on the agronomic, socio-economic, and political environment in which the farmers play a key role (Gutzler et al. 2015; Delecourt et al. 2019).

Population models, which integrate source-sink dynamics, may provide a valuable tool for risk assessors at the higher tier level of the risk assessment for nontarget arthropods (i.e., in situations in which no unacceptable risk can be demonstrated at the lower tier). By considering realistic surrogate landscapes with appropriate agronomic scenarios in line with the principles of Good Agricultural Practice, population models could be used at higher tier evaluations in conjunction with additional information, for example, from field data, to identify where and under what circumstances the use of specific plant protection products might be acceptable and where not (European Food Safety Authority 2014; Grimm and Thorbek 2014; Hommen et al. 2016). In some cases, to achieve an acceptable risk at a higher tier, the implementation of appropriate risk mitigation measures may be required (e.g., no application buffer zones, drift-reducing technology, reduced application rates or frequencies), which can be incorporated into the models; in the same way, models can be used to identify the most effective mitigation measures. For example, in Germany, drift mitigation measures can be reduced if the fields are located in an area that is federally indexed as containing a sufficient amount of seminatural structures (ecotones; cf. labeling phrases such as NT101 and NT102; German Federal Office of Consumer Protection and Food Safety 2020). This is an indirect incentive for farmers to maintain or create such structures. Beyond the regulatory risk assessment for plant protection products, there may be further applications of population modeling for the purpose of risk management. Taking the whole agricultural policy framework into account (e.g., the Sustainable Use Directive), the potential impact of changes to the landscape structure and modifications of cultivation systems on nontarget organisms could be evaluated with (meta)population models in a holistic approach.

Based on our literature review, the general conclusion that can currently be drawn is that metapopulation dynamics are more complex and more species and context dependent than presented by the different theoretical source-sink concepts. Furthermore, setting the appropriate time and spatial scales is considered to have an important impact when investigating metapopulation dynamics (Boughton 2000; Doak 2000; Johnson 2004; Talley 2007). External factors also impact the distribution of other species that can influence interspecies processes such as predator-prey interactions or competition

(see Cronin 2007; Rosenheim 2001; Benkman and Siepielski 2011). Thus identifying the influencing factors as well as the outcome for the population dynamics (including any source-sink effects) depends very much on detailed information on the life history of the model species concerned, species interactions, density-dependent processes, the direct effect of habitat diversity, habitat attraction, local agricultural practices (disturbances), and the impact of weather, as well as the temporal and spatial fluctuation of all these factors.

The EFSA Opinion (European Food Safety Authority 2015) pointed to the importance of source-sink dynamics and proposes that in European regulatory risk assessment, population models at the landscape level should be integrated into the risk assessment for plant protection products at the lower tier of the evaluation. The objective of a tiered risk assessment is to screen out uses at the lowest tiers that clearly present no unacceptable risk and to focus for the higher tiers on areas where such risks need more detailed evaluation. Given the numerous complex input parameters necessary and the high impact of landscape parameters (habitat diversity, agricultural practices, temporal and spatial fluctuation) on the outcome of population dynamics, the question should be asked whether such complexity is appropriate for the screening purpose of lower tier assessments. However, population models are useful for higher tier assessments to specify circumstances where concerns can be addressed and where not. This way, the models could be adjusted to a few species representative for identified concerns, taking into account the landscapes and Good Agricultural Practices relevant on a higher spatial and temporal resolution than in the lower tier risk assessment.

CONCLUSIONS

The present review on source-sink dynamics, with a focus on arthropods in agricultural landscapes, shows that there is a relatively large amount of available literature considering source-sink dynamics on a conceptual basis (theoretical or simulation models). In contrast, relatively few studies were identified that empirically demonstrated evidence for the existence of source-sink dynamics, and even fewer such studies focused on arthropods in agricultural landscapes. Our review also identifies the difficulty in drawing general conclusions on which factors (e.g., reproduction potential, mobility, habitat attraction, habitat diversity) are driving the strength and role of source-sink mechanisms on metapopulation dynamics, highlighting the complexity of metapopulation dynamics and their sensitivity to species characteristics and environmental variables.

The source-sink dynamic was introduced in the context of regulatory risk assessment of plant protection products by the EFSA (European Food Safety Authority 2015) with the simulation model for the carabid beetle *B. lampros* (Topping et al. 2015). This approach could be per se a valuable tool for higher tier nontarget arthropod risk assessment for plant protection products, when it comes to the assessment for specific agricultural scenarios. However, the available data we have summarized indicate that specific aspects of the

model species' life cycle, diversity in the landscape, and changes in time are crucial factors for the appropriate application of such models. In particular, it is important that the agricultural scenarios used in the simulation models be compliant with the European Union's efforts to make agriculture more diverse and sustainable.

Supplemental Data—The Supplemental Data are available on the Wiley Online Library at <https://doi.org/10.1002/etc.5137>.

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