BioControl (2017) 62:397–407
DOI 10.1007/s10526-017-9787-y

Spreading of alien species and diversity of communities

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Received: 29 March 2016 / Accepted: 18 January 2017 / Published online: 11 February 2017

Abstract A new species invading a new area may cause a decrease in diversity of the community already present there. Comparison of temporal changes in species diversity of the "new" community (including alien species) with those of the "original" community (including only native species) may clarify our understanding of the effect of alien species. Using a simulation-based modelling approach we considered several scenarios describing the invasion of native communities by alien species and calculated the trends in Shannon-Wiener indices and in the numbers of species of the "original" and "new" communities during the course of the invasion. We found that despite a large increase in the population size of the invasive alien species the diversity of the original community may be little affected. Native species numbers may stay relatively constant for a long time and then suddenly collapse. The results indicate some possibly still concealed consequences of the spread of the invasive ladybird *Harmonia axyridis* (Pallas).

Keywords Alien species · Native species · Ladybirds · Aphid predators · Simulation model · Community

Handling Editor: Helen Roy

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Introduction

Although the phenomenon of species extending their range is well known, intensive research on this topic only started in the late 1980s (Lockwood et al. 2007). Particularly important are invasive alien species that have a demonstrable ecological or economic impact (Snyder and Evans 2006; Lockwood et al. 2007). It is sometimes suggested that a new species invading a new area causes a decrease in diversity of the community already present there, but this has rarely been satisfactorily proven by empirical data (Bahlai et al. 2015; Honek et al. 2016). Preventing this decrease in diversity of native communities is a leading concern of conservation biology, which stimulated much research, dealing mainly with biological problems of species interactions. The empirical data for a direct test of such a decrease in diversity of native communities are missing, and very difficult to collect. Therefore, first some theoretical reasoning on the processes of temporal changes in dominance between species is useful. Comparison of temporal changes in abundance of species in a new community including alien species with those of the original community predicted by mathematical models may conceptually clarify our understanding of the effect of alien species.

The research presented here was motivated by (but is not specific to) *Harmonia axyridis*, an invasive ladybird species native to the east Palaearctic (Osawa 2011; Zakharov et al. 2011; Orlova-Bienkowskaja et al. 2015). It is a voracious predator of aphids, and therefore it was mass-reared and used in biological control of aphids in glasshouses. In the early 1990s, however, *H. axyridis* escaped from captivity and started to spread—first in North America (Bélanger and Lucas 2011), and later in Europe, South America and Africa (Lombaert et al. 2010, 2011; Sloggett and Honek 2012). In Western Europe, this invasion started after 2000 and is well documented in Great Britain since 2004 (Brown et al. 2008; Roy and Brown 2015). *H. axyridis* has now colonized a large part of the world, except for boreal and dry and wet tropical areas (Poutsma et al. 2008). The reasons for the worldwide success of *H. axyridis* are not yet completely understood, although several life history traits like preference for urban and agricultural habitats, wide diet breadth and thermal tolerance, high reproductive potential and genetic diversity are suggested as potential candidates (Roy et al. 2016).

It is reported that associated with the spread of *H. axyridis* in North America was a decrease in local aphid populations (LaMana and Miller 1996). Therefore, the economically positive impact of *H. axyridis* attracted less attention than its supposed negative impact on abundance and diversity of native aphidophagous species, particularly other coccinellids (Colunga-Garcia and Gage 1998; Fothergill and Tindall 2010; Koch and Costamagna 2016). This caused concern in Europe, where it was expected that *H. axyridis* would spread a few years later, which was soon realized. *H. axyridis* quickly became dominant in many host plant/prey systems and several short-term studies indicated a parallel decline in abundance of native species (Brown et al. 2011; Roy et al. 2012).

The widely proposed mechanism of these changes is intraguild predation, i.e., feeding of *H. axyridis* on other species of the aphidophagous guild, largely eggs and larvae of other species of coccinellids. In support of this idea, some direct natural (Hautier et al. 2011) and indirect laboratory experimental evidence (Pell et al. 2008; Hodek and Evans 2012) was presented. However, other mechanisms have been proposed to contribute to the success of *H. axyridis*: the species may be able (1) to exploit a wider range of species of aphids (Crowder and Snyder 2010) or of (2) extraguild prey than other ladybirds (Lucas and Rosenheim 2011). Several traits contribute to invasiveness of *H. axyridis* (Roy et al. 2016), including poly-voltinism supported by low diapause incidence (Reznik et al. 2015), wide diet breadth (Comont et al. 2012) including pest and non-pest insect species and fruits, fecundity equally high when fed with a variety of aphid and alternative prey (Guedes et al. 2016), resistance to starvation in a way that enables to cope with prey scarcity (Agarwala and Bhowmik 2011). There is no general agreement on which of these mechanisms play the dominant role, if any.

To summarize, the consequences of coccinellid invasions for communities of native species and the causes of changes are still not clearly understood (Evans et al. 2011). Despite some uncertainity and contradictory evidence (e.g. Harmon et al. 2007; Evans et al. 2011; Hemptinne et al. 2012), the conclusion accepted by most people is that both the abundance of species and diversity of native coccinellids decreases after invasion by *H. axyridis* and the usually accepted explanation of this effect is intraguild predation (e.g., Gardiner et al. 2011). Therefore, it is necessary to make a precise assessment of the impact of *H. axyridis* on native communities and predict future trends in both its numbers and those of its prey, serious agricultural pests: aphids. For this, sufficiently long population censuses before and after the invasion started are necessary, which do not exist (Kindlmann et al. 2011; Honek et al. 2013).

In such situations, the only way to predict the outcome of an invasion by this species on communities of native species is to use predictive simulation models. Although there are data demonstrating spread of *H. axyridis* into invaded areas (Roy et al. 2016), it is useful if the models are quite general. Despite their generality, however, such models may reveal a representative array of possible results and help us to understand changes in composition of the original coccinellid community after invasion not only of *H. axyridis*, but also other invasive alien species. These models provide criteria for evaluating the impact of invasive alien species on other species, i.e., for predicting how invasion of alien species may affect the diversity and numbers of other species. They may also demonstrate how these effects depend on the diversity of a native community, resistance of native species and competitive abilities of the invasive alien species. By assuming various properties of native and invasive alien species, we can suggest explanations for changes in biodiversity observed under natural conditions.

Here we used simulation models to investigate the diversity dynamics in a theoretical system consisting of an "original" community of native species and an invasive alien species that invades this community, thus creating a "new" community. We have considered five scenarios differing in (i) availability of "free" space within the original community, (ii) mode of interaction between alien and native species and (iii) distribution of the native species. We have calculated Shannon indices and numbers of species in the communities with and without the invasive alien species and looked at their trends during the course of an invasion.

Methods

A series of virtual native communities living in spatially-explicit landscapes was created by means of simulations. The simulations and all calculations were performed in Microsoft Excel. The Excel function RND() was used for creating random integers x with uniform distribution U(1, M) as x = ROUND(RND()*M,0).

We assumed $S = 24$ "native species" and a "community" (20 × 20 matrix) of "plants". Each element of the matrix was supposed to be inhabited by only one species. It was assumed that during the simulation either this species will survive or will be replaced by the invader. The algorithm of replacement is described below. In the model this was represented by a 20 × 20 matrix $M = \left(n_{i,j}\right)$, where $n_{\text{ij}} = s$ means that the population living in this element ("plant") belongs to species s, $s = 1, 2,\ldots,24$. A series of 400 "native populations" $P = (p_1, p_2,\ldots,p_{400})$, inhabiting the matrix was then created so that their species-abundance distribution followed a negative exponential, i.e., $y = a{\cdot}e^{-ax}$. This was achieved as follows. A series of random numbers $r_1, r_2,\ldots,r_{400}$, chosen form U(1, M) was generated. For each i, $i = 1, 2,\ldots, 400$ it was then set: if $\sum_{k=0}^{s-2} a \cdot e^{-ak} \le r_i \le \sum_{k=0}^{s-1} a \cdot e^{-ak}$, then $p_{\text{i}} = s$, for $s = 2, 3,\ldots,24$, and if $r_i \le a$, then $p_{\text{i}} = 1$. Using the Goal Seek Excel function, we found that $a = 0.12$ normalized the distribution for 24 species (i.e., $\sum_{k=0}^{24} a \cdot e^{-ak} = 1$).

The "populations" P were then placed into the matrix M using two scenarios:

(a) "*Random*", when elements of P were placed in M successively and each element of P was placed into a vacant element of M completely at random (using a random choice of i, j from U(1, M))—see Fig. 1 for an example.

(b) "*Aggregated*", when elements of P were placed in M successively by increasing species number, so starting from species 1 and ending with species 24, starting from the right bottom corner of the matrix ($n_{20,1}$) and continuing to the left top corner ($n_{1,20}$)—see Fig. 1 for an example.

The choices of the matrix rank and S were arbitrary, as the model is only illustrative. We did not aim to cover the whole generality of the problem by using the model. The resulting numbers of populations that belonged to particular species are shown in Fig. 2. Randomness (i.e., the numbers do not exactly fit a negative exponential) was due to using the random numbers from U(1, M).

Five scenarios of invasion were considered. All the elements of matrix M were always occupied by native populations [except for scenario (1)], which were distributed at random in the matrix [except for scenario (5)]:

(1) Some cells in the matrix were initially unoccupied (thus there were less than 400 native populations distributed at random) and the invader randomly occupied some of the empty cells. Random choice of the cells invaded by the alien species was achieved by repeated generating of random pairs of numbers i, j from U(1, M), until an empty cell n_{ij} was found. That is, no competition occurred, the invader just occupied empty niches as not all elements of matrix M were occupied by native species.

Fig. 1 Examples of population distributions in the matrix. *Numbers* indicate species number. *Top* "Random" and *bottom* "Aggregated" distributions of the population in the matrix

4	6	23	2	2	2	2	1	3	5	2	2	1	4	11	1	15	12	16	11
3	4	1	6	1	13	4	5	3	1	3	5	1	7	1	15	10	24	24	2
2	4	10	3	1	12	2	12	16	11	23	2	7	1	15	9	2	6	19	22
3	3	3	22	16	1	3	4	1	19	6	22	14	1	2	8	7	1	18	3
5	10	24	20	6	9	7	7	1	13	6	23	3	2	9	11	1	4	13	12
18	21	23	2	3	1	2	6	13	1	4	7	6	2	23	11	1	8	1	2
18	3	1	3	2	18	3	8	1	2	6	18	2	19	8	10	1	3	5	4
4	14	6	2	24	6	24	1	1	3	2	5	5	8	3	2	10	4	18	12
22	4	11	6	2	3	4	15	21	17	2	2	5	2	4	1	5	3	21	5
17	19	2	5	3	13	2	1	17	2	20	6	6	4	7	2	6	2	15	8
1	5	2	6	18	6	2	3	5	10	2	5	8	11	23	22	14	22	2	5
1	2	20	5	3	4	20	15	12	17	2	23	23	8	11	4	2	4	12	22
3	9	6	6	24	14	3	2	4	11	23	3	3	8	4	2	1	8	3	17
17	10	5	2	10	3	4	2	5	5	17	10	4	3	2	2	1	16	9	17
11	1	7	2	2	3	5	11	3	4	2	16	22	18	10	22	1	3	13	1
3	24	24	3	4	9	3	21	5	1	3	18	2	5	2	23	5	6	14	1
22	1	2	6	2	11	22	6	2	22	5	20	4	1	10	6	7	7	1	17
18	4	11	1	15	1	6	2	4	20	7	10	9	9	1	15	16	21	7	1
7	3	9	2	15	6	9	11	6	5	11	2	21	11	14	5	10	10	3	7
5	24	8	4	11	3	2	6	2	22	3	4	2	7	8	6	5	2	12	7

24	24	23	23	20	18	17	14	13	13	12	12	9	7	5	3	3	2	2	2
24	24	22	20	18	17	16	11	11	10	8	7	6	5	4	3	3	2	2	2
24	24	22	19	18	17	15	11	10	8	7	6	5	5	3	3	3	2	2	2
24	23	21	19	18	16	13	11	9	8	7	6	5	4	3	3	3	2	2	1
24	23	21	18	17	15	12	10	9	8	6	5	5	4	3	3	2	2	2	1
24	23	21	18	17	12	11	10	9	7	6	5	5	4	3	3	2	2	1	1
23	22	20	17	15	11	11	10	8	7	6	5	4	4	3	2	2	2	1	1
23	22	20	17	15	11	11	10	7	7	6	5	4	4	3	2	2	2	1	1
23	22	20	16	14	11	10	10	7	6	6	5	4	4	3	2	2	2	1	1
23	22	19	16	12	11	10	9	7	6	5	4	4	3	3	2	2	2	1	1
23	22	18	15	12	11	9	9	6	6	5	4	4	3	3	2	2	2	1	1
22	22	18	14	12	10	8	8	6	5	5	4	4	3	2	2	2	2	1	1
22	22	17	14	11	10	8	8	6	5	5	4	4	3	2	2	2	2	1	1
22	21	16	13	11	10	8	7	6	5	5	4	3	3	2	2	2	1	1	1
22	20	15	13	11	8	7	7	6	5	4	4	3	3	2	2	2	1	1	1
21	18	15	12	10	8	7	6	6	5	4	3	3	3	2	2	2	1	1	1
21	17	14	11	9	7	6	6	6	4	4	3	3	3	2	2	2	1	1	1
19	15	13	10	9	6	6	5	5	4	3	3	3	2	2	2	2	1	1	1
18	15	11	9	7	6	5	5	5	4	3	3	3	2	2	2	1	1	1	1
16	14	6	6	6	6	5	4	4	4	3	3	2	2	1	1	1	1	1	1

(2) Cells occupied by the dominant native species were invaded and the native species replaced by the "strong" invader (an invasive alien species, which after its introduction first exterminates the dominant, most abundant native species). Random choice of the cells invaded by the invader was achieved by repeated generating of random couples of numbers *i, j* from U(1, *M*), until a cell occupied by the dominant species (species 1) n_{ij} was found.

(3) Cells occupied by the rarest native species were invaded, native species was replaced by the "weak" invader (a species that after introduction first exterminates rare native species). Random choice of the cells invaded by the invader was achieved by repeated generating of

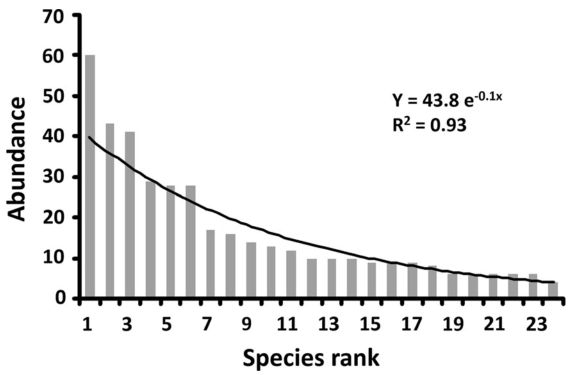

Fig. 2 The resulting species-abundance distribution (numbers of individuals ranked by abundance) used in the model

random couples of numbers *i, j* from U(1, *M*), until a cell n_{ij} occupied by the rarest species (species 24, 23, etc.,) was found.

(4) Invaded cells were chosen at random within the whole matrix *M*, independently of the native species present and the native species was replaced by the invader.

(5) Initial distribution of the native species was aggregated. Invaded cell was chosen at random within the whole matrix *M*, independently of the presence of the native species and native species were replaced by the invader. Thus not all elements of matrix *M* (all native populations) were distributed at random in the matrix.

In the following, we use the name "original community" for the set of species that were present before the community was invaded and "new community" for the set of species consisting of those present before the invasion and the invasive alien species. Of course, the number of species that were present before invasion decreased or at least remained constant after the invasion. We calculated the following diversity measures for each of the communities considered:

(i) Number of native species surviving to a particular stage of invasion,
(ii) Shannon-Wiener index H of the "new community",
(iii) Shannon-Wiener index H of the species surviving from the "original community".

We also calculated other diversity indices (Simpson's D and E, Shannon's equitability), but the results were qualitatively similar and therefore are not presented here.

Results

Results for scenario (1) are shown in Figs. 3 and 4. Figure 3 shows that the more empty niches there are before invasion, the lower the diversity after invasion when alien species occupy all of the empty spaces. Figure 4 shows that diversity in the new community plotted against percentage of the cells (niches) empty before the invasion and occupied by the invasive alien species, first increases and then declines. The same dependence plotted for the original community is constant, i.e., shows no trend.

Results for scenario (2): "strong" species invades and the native species are replaced by the invader. The invader first replaces the most abundant species, when all its individuals are replaced, then the second most abundant species is replaced etc., until all invaders are placed in the matrix. The results are shown in Fig. 5. Diversity in both the original and new communities declines with the percentage of cells occupied by the invader. However, diversity in the new community, including the invasive alien species, decreases faster than that in the rest of the original community.

Results for scenario (3): "weak" species invades and native species are replaced by the invader, starting with the rarest, as shown in Fig. 6. With increase in the percentage of cells occupied by the invader, diversity

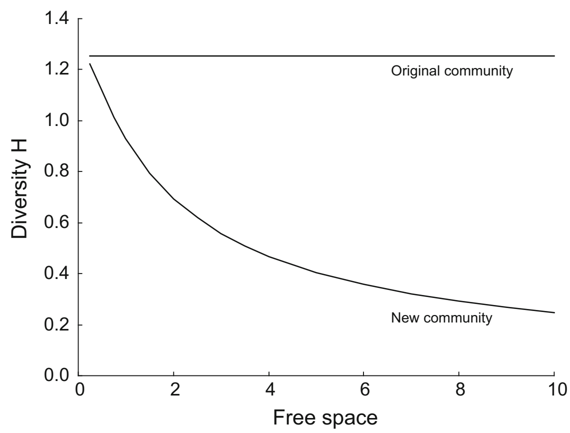

Fig. 3 Results for scenario (1): invasion without competition. Diversity in the "original community" is not affected because the invasive alien species only occupies the empty niches. Diversity in the "new community" decreases. The more empty niches, the lower the diversity (as the invader becomes more dominant, diversity in the new community declines). H is the Shannon-Wiener index. "Free space" on the *x*-axis means number of free cells occupied by the invader

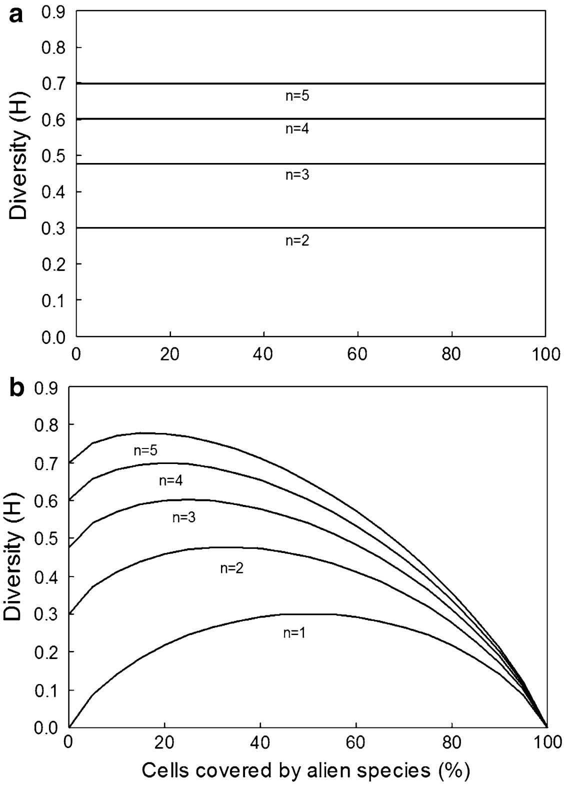

Fig. 4 Results for scenario (1): invasion without competition. **a** Diversity in the original community and **b** diversity in the new community, plotted against percentage of empty niches present before invasion and then the area occupied by the invasive alien species. Number *n* indicates the number of species in the original community. H means the Shannon-Wiener index

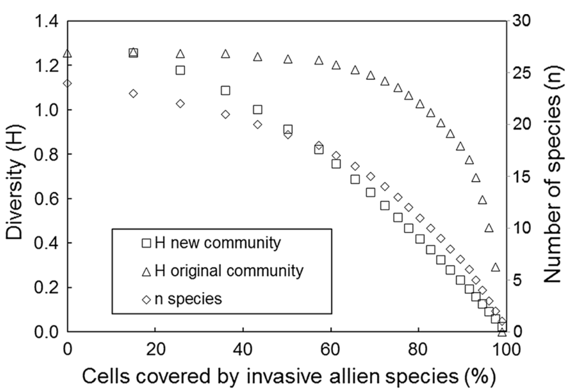

Fig. 5 Results for scenario (2): "strong" species invade, native species replaced by the invader starting with the most abundant. Diversity in the original community including species that were present before the invasion (H original community), diversity in new community consisting of species present before the invasion and the invasive alien species (H new community), and number of species surviving in the community (proportion from the original n of the species) decline with the percentage of empty niches occupied by the invader

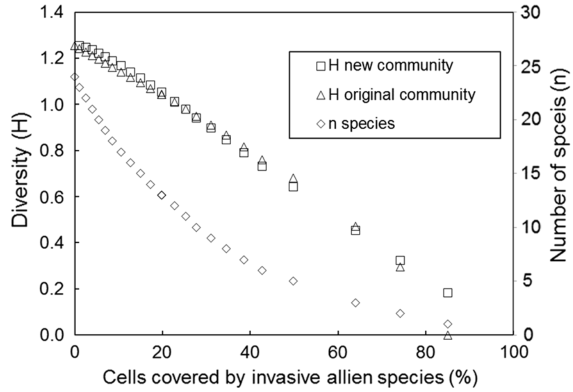

Fig. 6 Results for scenario (3): "weak" species invade, native species populations (cells) replaced by the invader starting with the rarest. Diversity in original community including species that were present before the invasion (H original community), diversity in new community consisting of species present before the invasion and the invasive alien species (H new community), and number of species surviving in the community (proportion from the original n of the species). H means the Shannon-Wiener index

in the new community H new declines as in the original community (H original). The proportion of remaining native species (n species) decreases strongly during the early stages of invasion (when the number of cells occupied by the invader is still low).

Results for scenario (4): invaded cells chosen at random and native species replaced by the invader, resulting in random distribution of the native species as shown in Fig. 7. With increasing area occupied by the invasive alien species, diversity in the new community first slightly increases, then decreases. Diversity in the native community remains constant and only decreases when the invader is very abundant.

Results for scenario (5): invaded cell chosen at random and native species replaced by the invader, resulting in an aggregated distribution of the native species as shown in Fig. 8 for two sub-scenarios: (i) invasive "strong" species spreads where dominant native species is present (forming large patches) and (ii) invasive "weak" species spreads where rare native species are present (forming small patches). In both cases, as the percentage of area colonized by the invader increases, diversities in both the original and new communities decline. Diversity in the new community declines more rapidly (sub-scenario i) or less rapidly (sub-scenario ii) than that in the original community.

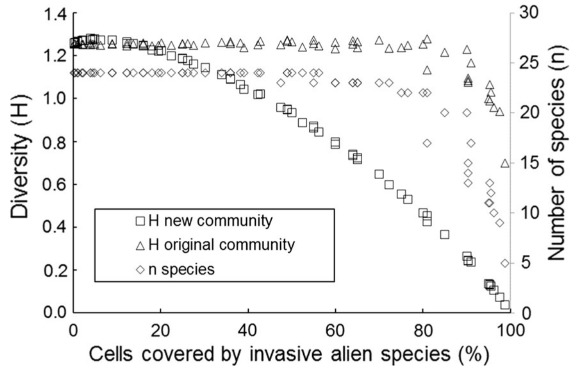

Fig. 7 Results for scenario (4): invaded cell chosen at random, native species populations (cells) replaced by the invader, random native species distribution. Diversity in original community including species that were present before the invasion (H original community), diversity in new community consisting of species present before the invasion and the invasive alien species (H new community), and number of species surviving in the community (proportion from the original n of the species). H means the Shannon-Wiener index

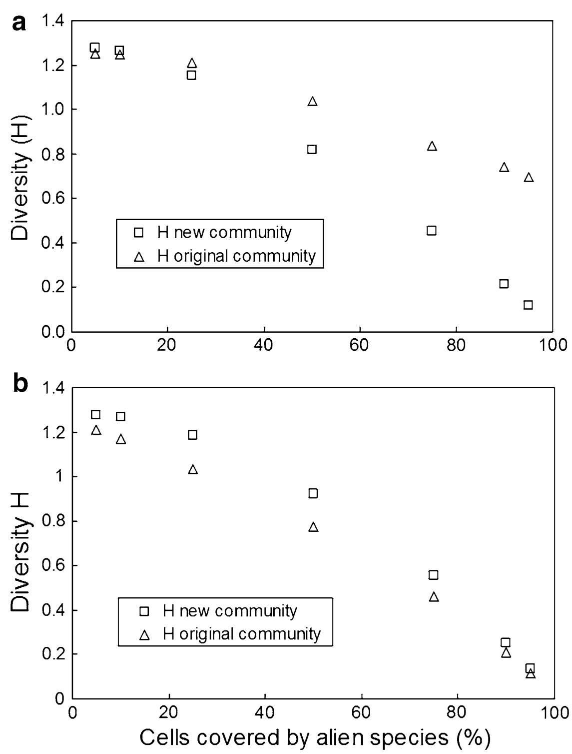

Fig. 8 Results for scenario (5): invaded cell chosen at random, native species replaced by the invader, aggregated native species distribution—for two sub-scenarios: **a** invasive "strong" species spreads where dominant species are present (and forms large patches) and **b** invasive "weak" species spreads where rare species are present (and forms small patches). H means the Shannon-Wiener index

Discussion

In this paper we consider application of a general model describing a simple situation when an invasive alien species replaces patches occupied by native species under different assumptions on distribution of native species and invasiveness of the invasive alien species. This model nicely illustrates invasion of *H. axyridis* into communities of native aphidophagous coccinellids. As empirical data describing the course of invasion of a native community are scarce, we do not know which of the modelled scenarios should be adopted: whether or not the invader attacks individual "patches" occupied by native species at random or replaces only certain species—either the dominant or rare ones. Analysis of the model draws attention to some overlooked details of the process of spread of invasive alien species (especially *H. axyridis*) within communities of native coccinellids. We show the differences between results obtained when the characteristics of the community, species richness and diversity, are evaluated for community of native species only or for the "new" community including also the alien species. We then investigate the course of decrease in native species number and diversity of native and "new" community with increasing abundance of the invader species. We also illuminated how the invasive alien species affects diversity and species richness of the "new" community depending on the diversity of native community.

Our results for scenario (1) show that the more empty niches there are before invasion, the lower the diversity after the invasion when invasive alien species occupy all of the empty spaces. Biologically this means that as the invader becomes more dominant, diversity in the new community declines, although diversity in the original community (native species) is not affected. An example of such scenario may be the *Adalia bipunctata* invasion to Japan, where this species avoided interspecific competition with the dominant *H. axyridis* by desynchronization of its occurrence during the vegetative season, and competition with *Coccinella septempunctata* by habitat segregation (Toda and Sakuratani 2006). In local populations, *A. bipunctata* occurred in different proportions (0.1–0.8 of the total amount of coccinellids) without any systematic effect on the diversity of the remaining native coccinellid community.

If the invader randomly occupies some of the empty patches, diversity in the new community first increases and then, as the invader spreads, declines. The effect of invasive alien species on coccinellid community after invasion is demonstrated by changing the diversity of the community of native species and the “new” community including both native and invasive alien species, which is demonstrated after recalculating data of several studies concerning several invasive alien species including *H. axyridis*. Invasive alien species cause an increase of the diversity of native coccinellid communities strongly, when the native community consists of only few species (Alyokhin and Sewell 2004) or when the abundance of the invasive alien species remains low (Diepenbrock and Finke 2013; Gardiner et al. 2014). The diversity of the “new” community decreases during the course of invasion only when the invasive allien species becomes abundant. Such transition from a “positive” to a “negative” effect of invasive alien species on community diversity may appear rather abruptly, early after arrival of invasive allien species (Panigaj et al. 2014; Honek et al. 2016). In other cases, the diversity of the “new” community decreases gradually with time elapsed since invasion, in parallel with increasing abundance of the invasive alien species (Grez et al. 2016).

The more diverse the original community, the smaller is the initial increase in diversity after the introduction of the invasive alien species and the less steep is then the decrease in diversity as the abundance of species increases. These predictions conform to experimental data (Evans 2016). The existence of empty niches for invasive alien species is not just a theoretical assumption. Empty niches originate as a consequence of spatial (Gillespie and Roderick 2002) and temporal changes in host utilization (Gidoin et al. 2015). An invasive alien species spreading into a new area causes a decrease in the diversity of the community present. This stimulated much research, dealing mainly with biological problems of species interactions. The discussion of how invasive alien species affect original communities becomes especially important with respect to the spread of the invasive ladybird *H. axyridis*, as it is usually expected to affect native ladybird communities adversely (Brown et al. 2011).

If native species in a patch are replaced by an “strong” invader, i.e., if the invasive alien species exterminates the dominant species, with increasing area occupied by the invasive alien species, diversity in the new community first slightly increases and then decreases. Diversity in the native community remains constant and decreases only when the invader is very abundant. If native species in a patch are replaced by a “weak” invader, which exterminates rare native species, diversity in the new community changes in similar way as it does in the original community but the number of species that survive decreases faster than when the invader is “strong”. Considering predictions of scenarios (2) and (3) we think it is useful to consider separately the contrast between the effect of “strong” and “weak” species, which are extremes of a continuum of competitive behaviour that includes direct competition (Roy et al. 2016) and indirect effects (With et al. 2002; Das and Dixon 2011; Dixon and Kindlmann 2012). Extermination of *A. bipunctata* from communities of Western and Central Europe would be an example of scenario (2) if *H. axyridis* were its cause. However, this is unlikely (Honek et al. 2016). Other examples of scenarios (2) and (3) are difficult to retrieve from published literature apparently because invasive alien species affect most if not all native species, each with different intensity and effect. However, scenarios (2) and (3) are useful models for detecting effect of a “specialist” predator on the course of community change.

The most probable course of replacement of native by invasive alien species is scenario (4) in which the invasive alien species replaces patches of native species at random. Diversity in the new community decreases (because of the spread of the invasive alien species), while that in the original community (native species) decreases only at the final stage of the invasion, in parallel with a slow decrease in the number of native species. The results of scenario (5) show that the effects of the distribution of the original community (random or aggregated) are small.

Our results show that diversity changes over time during an invasion because of the increasing dominance of the invasive alien species, but the effect on the species already present may vary. Despite a large increase in numbers of the new invasive alien species, the diversity in the original community may be little affected (Gardiner et al. 2013, 2014). The extent of the effect depends on several factors, including presence of free space (niches available for invasive alien species, which are not occupied by native species distribution of species in the original community, and types of interaction between alien and native species. As in scenario (1), adding an invasive alien species to an established community of "native" species initially positively affects the diversity in the community. This increase in diversity slows down as the invasive alien species spreads. Diversity then starts to decrease and finally converges to zero, when the invasive alien species replaces all native species. A corollary is that the diversity in the new community may decline with little or no parallel change in the diversity in the original community of native species. This is very important in cases when native species become rare before the arrival of an invasive alien species and leave "free space" for its spread, because other drivers of population change may play a role, like habitat deterioration or climate change (Didham et al. 2007; Dixon and Honek 2014; Bahlai et al. 2013; Honek et al. 2016; Diepenbrock et al. 2016).

The process of colonization of an area by an invasive alien species affects the diversity in the community. The magnitude of this effect depends on the proportion of the available "space" that the invasive alien species occupies. Our simulations revealed a particularly interesting situation that occurs when native species are replaced randomly. In this case the diversity in the "original" community for long time did not reflect the increase in abundance of invasive alien species, except at the final stage, when nearly all cells are occupied by the invasive alien species. This conservative behaviour may call for cautious interpretation of the small changes in species diversity observed in native communities after the invasion by *H. axyridis* in Central Europe (Honek et al. 2013, 2016). Minute differences may conceal an advanced stage of the *H. axyridis* invasion that might have negative consequences for the "original" community in future.

Our study conceptually clarifies several situations, which differ in important characteristics: availability of free space within the original community, competitive relationship between the invasive alien and native species and distribution of native species, without entering into details of biology. Further, this study investigates separately the diversity in the "original community", i.e., the community of native species, which survive during the process of invasion of an invasive alien species, and diversity in the "new community", which includes native species and invasive alien species. This distinction has interesting implications, because the trajectories of the change in diversity in the "original" and "new" community substantially differ in many situations.

Acknowledgements This research was supported by the Grant No. 14-26561S of the GA CR and by the MSMT within the National Sustainability Program I (NPU I), Grant No. LO1415.

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