



Research Article

## Road and railway verges serve as dispersal corridors for grassland plants

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### Abstract

The role of linear habitat strips as dispersal corridors is a disputed topic. Reports concerning their significance for animals have been contradictory, and the functions of corridors have been difficult to study in the case of sedentary organisms such as plants. Previous studies on dispersal of plants along corridors have concentrated on a single or a few species at a time. We developed a general method, a generalisation of the binomial test, for considering dispersal or spatial relations of a large group of species. Particularly, we studied the ability of grassland plants to spread along road and railway verges. Our data set consists of plant lists collected at study plots scattered irregularly along road and railway networks. The dispersal ability was assessed by testing whether the species composition at neighbouring sites – measured along roads and railways – reflects spatial dependence within each species. Our result showed that similar combinations of grassland species occurred at neighbouring sites more often than expected in a spatially independent case. We argue that management of verges and spatial autocorrelation of environmental factors were not responsible for the result and thereby we conclude that grassland plants use road and railway corridors for dispersal. This result is encouraging in regards to preservation of grassland plant populations. Although semi-natural and natural grasslands have become scarce, road and railway embankments may partly compensate for this loss, serving as substitute habitats and dispersal routes.

### Introduction

Various habitat strips, such as hedgerows, road and railway verges and different greenbelts are frequently called corridors. The term corridor implies that organisms move from place to place along these elongated landscape elements. Corridors are often deemed to have a positive effect on species persistence and dispersal (e.g., Saunders and Hobbs 1991; Meffe and Carroll 1994). On the other hand, the costs and limitations of corridors are also well recognised (e.g., Simberloff et al. 1992; Mann and Plummer 1995). They may facilitate movement of undesirable organisms, for instance predators and pests, and they may even fail to increase migration or to prevent extinctions.

Based on field observations, several animal species have been reported to use corridors for moving or simply as habitat (Bennet 1990; Haas 1995; Lynch et al. 1995; Downes et al. 1997). Although using corridors, for example kangaroos, butterflies and salamanders are also able to move across the matrix habitat (Arnold et al. 1991; Sutcliffe and Thomas 1996; Rosenberg et al. 1998). The presence of corridors has, nevertheless, been experimentally shown to slow down extinction rates of such organisms as *Drosophila* flies (Forney and Gilpin 1989), ciliata (Holyoak and Lawler 1996) and microarthropods (Gilbert et al. 1998). These results suggest that corridors may have positive effects on the persistence of populations and metapopulations.

In regards of plant dispersal or population maintenance, direct evidence for the significance of corridors is difficult to obtain due to the sessile nature of plants. Despite this, a number of generalisations have been made on the basis of field observations and transplantations. For instance, fencerows fail to serve as movement corridors for woodland plants, owing to their poor quality as habitat (Fritz and Merriam 1993). Conversely, annual exotics can effectively invade natural areas along corridors of disturbed vegetation (Zink et al. 1995). A few maritime or wetland species have similarly been observed to spread to inland areas along sandy road and railway verges and along ditches (Suominen 1970; Scott and Davison 1982, 1985; Wilcox 1989). Seeds of plants belonging to flora of roadsides have also been shown to be carried along roads by moving vehicles (Schmidt 1989).

Road and railway verges, normally being open, well-lighted and regularly mown areas are potential habitats for grassland species adapted to continuous disturbance. Semi-natural grasslands constitute a threatened, declining habitat type in Northern Europe (Bengtsson-Lindsjö et al. 1991; Eriksson et al. 1995; Rassi et al. 2000), and suitable alternative habitats are needed for survival of grassland plant populations. In fact, several grassland species do occur in Finnish road and railway corridors (e.g., Anon. 1996a,b). However, if the matrix environment is unsuitable, the migration of grassland plants along corridors is ineffective, since high quality habitat patches are scarce and these plants often lack adaptations to wind dispersal (van Dorp 1996; van Dorp et al. 1997). Compared to Central Europe where the landscape matrix consists of agricultural fields and settled areas (Jennersten et al. 1992), the structure of landscape is mainly reversed in the boreal region. Woodlands cover about 75% of land area in Finland (Sevola 1997) while fields and grasslands form sparsely scattered islands within this matrix. Moreover, forests in the study area are relatively species-poor and normally dominated by pine (*Pinus sylvestris*) or spruce (*Picea abies*). Because of heavy shading and acidic soil they are hostile environments for grassland plants, traffic route verges being more potential habitats and dispersal routes.

We used field data to study whether grassland plants as a group are able to use road and railway verges as dispersal corridors. To the best of our knowledge, there are no previous studies focusing on dispersal of a group of plant species as an entity, instead of single species. Since our data were collected during one summer only, we were not able to follow the dis-

persal of the species in time. Instead our aim was to recognise the dispersal mechanism from the species-specific spatial patterns formed by the inhabited and uninhabited study plots scattered along roads and railways. Populations along roadsides may originate from seeds occasionally arriving within road construction materials or seed mixture sown on verges. If these were the only ways for new populations to arise, the inhabited study plots should form a spatially random pattern. Seeds may also disperse from the surroundings resulting in plant communities deterministically resembling those of the adjacent habitats. However, if the plants also spread using traffic routes as corridors, this should be reflected as similarity in the flora at nearby study plots (measured along the roads and railways) regardless of the surrounding habitats. The key question addressed here was: Is the species composition at neighbouring plots more similar than would be expected if the plots were inhabited independently? To this end we applied a generalisation of the binomial test.

## Materials and methods

The vegetation data used in this study were initially collected in order to compare the species composition of road and railway verges to that of semi-natural grasslands (Tikka et al. 2000). The study was conducted from June to August 1997 in central Finland (62° N, 27° E), in an area 115 km from west to east and 57 km from south to north. Using topographic maps (1:20 000), we selected 90 study sites along three different types of traffic routes: 31 along paved main roads, 29 along gravel roads and 30 along railways. Each site consisted of a 200 m long strip of embankment on one side of a road or a railway. One half of the sites, of each traffic route type, were located in a cultural environment with fields or settlements and the other half in a forested environment. We avoided selecting several sites along the same road if possible. However, owing to the sparsity of the railway network, a few sites had to be placed along each railway. The distances between sites were not considered at this stage, and therefore they vary randomly. To acquire information about construction and management of road and railway verges, we consulted the Finnish National Road Administration and Finnish Railways.

At each site, we recorded all the vascular plant species growing between the rails or road edge and the border of the adjacent forest, field or building lot.

For this study, we included only the species adapted to conditions on traditionally managed grasslands. These grassland species have been identified by long-term monitoring of their performance on regularly managed, as well as, abandoned and closing grasslands (Ekstam and Forshed 1997). The nearest neighbour for each site was defined as the site with the shortest distance measured along intersecting traffic routes. If two sites formed a symmetric pair being the nearest neighbours to each other, this pair was included only once. Each of the grassland species growing at the first site of the pair was recorded as present or absent at the other site.

To study the spatial randomness of inhabited sites for each species, we applied the binomial test ('coin tossing') generalised as follows. For simplicity, let us first consider a case of only one species with  $n$  inhabited sites, where  $1 < n < N$ ,  $N$  denoting the total number of sites. The occurrence of the species at the nearest neighbours of the inhabited sites reflects the spatial dependence. Let  $n^*$  stand for the number of those inhabited sites whose nearest neighbours were checked (for some species  $n^*$  may be less than  $n$  since the symmetric pairs were counted only once). Under complete spatial independence the (conditional) probability of having an inhabited neighbour would be  $(n - 1)/(N - 1)$ . Hence the parameters of the corresponding binomial test are  $n^*$  as the number of trials ('tosses') and  $p = (n - 1)/(N - 1)$  as the probability of a success ('head') in one trial. The distribution of the number of successes, that is, the inhabited neighbour pairs, is asymptotically normal with mean  $n^*p$  and variance  $n^*p(1 - p)$ .

Instead of studying single species, our aim was to test the patterns of a group of  $I$  species as a whole. Therefore, we had to generalise the formulae above for several species having individual success probabilities  $p_i$ ,  $i = 1, 2, \dots, I$ . Let  $n_i$  denote the number of inhabited sites for species  $i$ ,  $n_i^*$  the corresponding number of test sites,  $p_i = (n_i - 1)/(N - 1)$  the probability of a success, and  $m_i$  the number of neighbour pairs inhabited by species  $i$ . (The analogy to coin tossing is such that we have  $I$  coins with individual probabilities for 'head'. We toss each coin  $n_i^*$  times and count the total number of 'heads'.) Let  $m = \sum_{i=1}^I m_i$  stand for the total number of neighbour pairs such that both are inhabited by the same species (summed over all  $I$  species). Assuming, in addition to the spatial randomness within each species, that the species grow and disperse independently of each other, the expected value  $\mathbf{E}(m)$  of  $m$  can be written as

$$\mathbf{E}(m) = \mathbf{E}\left(\sum_{i=1}^I m_i\right) = \sum_{i=1}^I \mathbf{E}(m_i) = \sum_{i=1}^I n_i^* p_i.$$

In other words, the expectation of the sum over all species equals to the sum of the species-specific expectations – the assumed independence between species allows for changing the order of the operations. The same applies to the variance of  $m$ :

$$\begin{aligned} \text{Var}(m) &= \text{Var}\left(\sum_{i=1}^I m_i\right) = \sum_{i=1}^I \text{Var}(m_i) \\ &= \sum_{i=1}^I n_i^* p_i (1 - p_i). \end{aligned}$$

Assuming the species mutually independent with respect to their occurrence and dispersal is obviously not correct, but this technical assumption enables us to exploit the data of several species simultaneously through the formulae above. In nature, some species benefit from the occurrence of other species – for instance by parasitism – while some species may have allelopathic relations with each other. As our data include dozens of species growing together in different mixtures depending on the site, we presume that the total effect of these contrasting dependencies does not falsify the results considerably. In practise, it is more important to know whether the grassland species are able to disperse along corridors than whether individual species disperse independently of the other species.

As already mentioned, the distribution of the number  $m_i$  of neighbour pairs inhabited by a species  $i$  is asymptotically normal in the spatially random case. The same holds – even better – to  $m$  being a sum of several such variables with mutual independence. Therefore we may assume, given the spatial randomness, that  $m$  follows a normal distribution with the expectation and the variance as formulated above.

It is not reasonable to assume spatial inhibition as an option in the vegetation patterns, that is, the same species typically avoiding growing at neighbouring sites. Hence, a one-sided test is appropriate here with hypotheses  $H_0$ : occurrence of species at the study sites is spatially independent, or, observed  $m_{\text{obs}} = \mathbf{E}(m)$ , and  $H_1$ : the neighbouring sites tend to have similar flora, or,  $m_{\text{obs}} > \mathbf{E}(m)$ .

To consider also the effect of the distance between the neighbouring sites to the similarity of their flora, we proceeded as follows. Firstly we approximated the expected number of species in common at two neighbouring sites given the number of species observed

at these sites and assuming no spatial association between the sites. The approximation formula is derived in Appendix 1. Then we compared the expected and observed numbers of shared species in relation to the mutual distance between the sites.

## Results

The data were comprised of 61 pairs of nearest neighbours. The distance between these neighbours varied from 400 m to 11 km (median = 1.9 km). In all, 78 grassland plant species were identified at the study sites. Of these, 11 species occurred only once and had to be excluded from the statistical consideration since their potential ability to spread along verges could not be assessed on the basis of a single occurrence. Consequently, 67 grassland species (Table 1) were used to test the similarity of species composition between neighbouring sites. For individual species, the number of inhabited sites varied between 2 and 82 (mean = 33). Respectively, the number of pairs of neighbouring sites inhabited by the same species ranged from 0 to 54 (mean = 14). The sum over all species was  $m_{\text{obs}} = 929$ . The expected value of the corresponding spatially independent case was  $E(m) = 875$  with variance  $\text{Var}(m) = 291$ . These parameter values yield the (standardised normal) test statistic of 3.16 corresponding to  $P = 0.0008$ . Hence the species composition at the nearest neighbouring sites was significantly more similar than would be expected if the species inhabited the sites with no spatial dependence. This result is illustrated in Figure 1, where the observed and expected numbers of species at neighbouring sites are shown as a function of the distance between the neighbours.

When running the test separately for each of the three main dispersal groups presented in Table 1 (wind, animals, unassisted), the results were of similar type as for all the species together. Even though the sample size dropped to only one third of the original, in the group of unassistedly dispersing species the power of test was adequate to produce the test statistic of 3.69 with  $P = 0.0002$ . Nevertheless, each dispersal group included species for which the observed number of occupied neighbouring sites was higher than expected if the sites were occupied randomly. For instance, the expected and observed numbers were 50 vs. 54 for *Achillea millefolium*, 19 vs. 27 for *Phleum pratense* and 33 vs. 37 for *Lathyrus pratensis*.

In the preceding tests the focus was on studying the pairs of neighbouring sites, independent of their

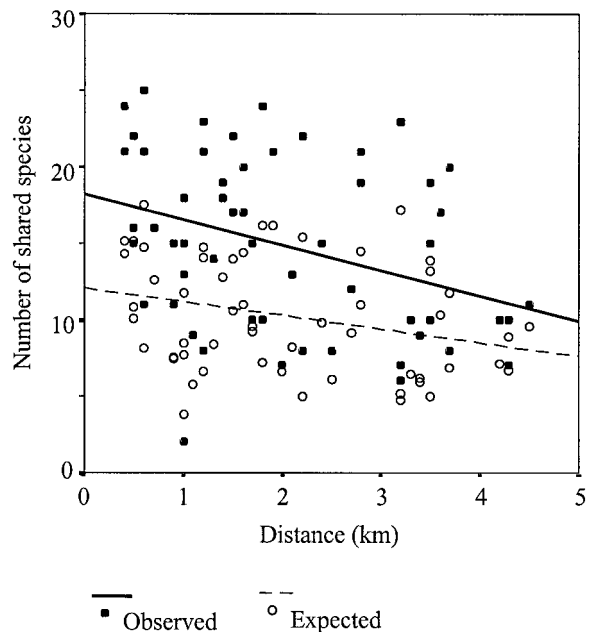


Figure 1. The expected and observed numbers of shared species at the pairs of neighbouring sites as a function of the mutual distance between the sites. The corresponding linear regressions are shown. Calculation of the expected species numbers is explained in Appendix 1.

mutual distance. In Figure 1 the expected numbers, as well as the observed numbers of the species shared at the same pairs of sites are plotted against the distance between the sites. The observed number of same species at neighbouring sites declined with growing distance between the sites. At all distances, however, it tended to be higher than the corresponding expected number. In Figure 1 we concentrated on distances less than five kilometres, the few neighbour pairs with a longer mutual distance clearly being outliers.

## Discussion

The occurrence of grassland species in our data were shown to be far more similar at neighbouring sites compared to a distribution pattern reflecting spatial independence among sites. Even though the number of shared species declined with growing mutual distance of neighbours, up to five kilometres it remained at a higher level than expected with no spatial association between the pairs of sites. This supports our hypothesis that grassland species disperse along road and railway verges. Since the value of our test statistic is highly significant, it even allows the potential

Table 1. Grassland species in this study. Nomenclature is according to Hämet-Ahti et al. (1998). The letters after names of species define dispersal mechanism, if known: Wm = wind, assisted by morphological features such as wings; Ws = wind, because of small seed size; Aa = animals, attached on them; Af = animals, used as food; U = unassisted, lacking features assisting dispersal (after Grime et al. 1988).

<i>Achillea millefolium</i> Wm	<i>Elymus repens</i> U	<i>Pimpinella saxifraga</i> U
<i>A. ptarmica</i> Wm	<i>Equisetum fluviatile</i> Ws	<i>Poa pratensis</i> U
<i>Agrostis canina</i> Aa	<i>Euphrasia stricta</i> Ws	<i>P. trivialis</i> U
<i>A. capillaris</i> U	<i>Festuca ovina</i> Aa	<i>Polygonum aviculare</i> U
<i>Alchemilla filicaulis</i> Aa	<i>F. rubra</i> Aa	<i>Potentilla argentea</i> U
<i>A. monticola</i> Aa	<i>Fragaria vesca</i> Af	<i>Prunella vulgaris</i> Aa
<i>Alopecurus aequalis</i> U	<i>Galium uliginosum</i> U	<i>Ranunculus acris</i> Aa
<i>A. geniculatus</i> U	<i>Geranium sylvaticum</i> Aa	<i>Rhinanthus minor</i> Wm
<i>Antennaria dioica</i>	<i>Geum rivale</i> Aa	<i>R. serotinus</i> Ws
<i>Anthoxanthum odoratum</i> Aa	<i>Glyceria fluitans</i> U	<i>Rumex acetosa</i> Wm
<i>Bistorta vivipara</i> U	<i>Gymnadenia conopsea</i> Ws	<i>R. acetosella</i> U
<i>Calluna vulgaris</i> Ws	<i>Hieracium umbellatum</i> Wm	<i>Sagina procumbens</i> U
<i>Campanula cervicaria</i> U	<i>Juncus conglomeratus</i> Aa	<i>Salix repens</i> Wm
<i>C. persicifolia</i>	<i>J. effusus</i> Aa	<i>Stellaria graminea</i> U
<i>C. rotundifolia</i> Ws	<i>J. filiformis</i> Aa	<i>Trifolium medium</i> Aa
<i>Carex nigra</i> U	<i>Juniperus communis</i> Af	<i>T. pratense</i> Aa
<i>C. pallescens</i> U	<i>Lathyrus pratensis</i> U	<i>T. repens</i> Aa
<i>Centaurea jacea</i> U	<i>Leontodon autumnalis</i> Wm	<i>Veronica chamaedrys</i> U
<i>Cirsium helenioides</i> Wm	<i>Leucanthemum vulgare</i> U	<i>V. officinalis</i> U
<i>C. palustre</i> Wm	<i>Luzula multiflora</i> Af	<i>Viola canina</i>
<i>Dactylorhiza maculata</i> Ws	<i>Lychnis flos-cuculi</i> Ws	<i>V. palustris</i> Af
<i>Deschampsia cespitosa</i> Aa	<i>Myosotis scorpioides</i> U	
<i>Dianthus deltooides</i> U	<i>Phleum pratense</i> Aa	

dependencies between some of the species. The assumption of mutual independence of species is related to the generalisation of binomial test, but in nature the concept of dispersal itself is of importance. Whether the species disperse alone or not does not affect the spatial pattern observed in this study. In the following we focus on alternative explanations to the observed phenomenon of floristic similarity in the neighbouring sites.

Sowing of road verges might appear to explain the occurrence of same species at nearby sites. Among the 61 pairs of nearest neighbours in the data, however, there were only five cases in which both sites within the pair had been sown. In all these pairs, sowing had been performed before the year 1975 at one or both of the sites. The seed mixture has varied in both composition and species proportions but has always contained less than 10 species. Seeds of only three grassland species identified here have been included since the beginning of management by sowing: *Festuca rubra*, *Poa pratensis*, and *Trifolium repens*

(Anon. 1991, 1998; G. Strandström, personal communication). The coverage of sown species tends to decrease over time, and only *F. rubra* remains abundant a few years after sowing (Suominen 1974). With the existence of as few as five pairs of nearest neighbours in which both sites had been sown, and with most of these sowings performed over 20 years ago, sowing is a negligible factor resulting in the observed high similarity of species composition at nearby sites.

Patchy distribution of both abiotic and biotic environmental factors in the surroundings of the sites, i.e. spatial autocorrelation, could cause the observed similarity of vegetation at neighbouring sites (Legendre 1993; Brown et al. 1995). However, this is not likely for the following reasons. First, in the majority of neighbour pairs of this study (34 out of 61) the sites were not located in similar environment but one of the sites was in a forested and the other in a cultural habitat type. If spatial autocorrelation was the main factor affecting the species composition, this should lead to dissimilarities at neighbouring sites, as

the surrounding environment has been shown to affect species composition along the studied roads and railways (Tikka et al. 2000). Second, the distances between nearest neighbours were considerably long and variable ranging from a few hundred metres to several kilometres. The relatively large scale emphasises the mutual independence of the sites with respect to their surroundings. Furthermore, even though the type of traffic route itself has an effect on species composition (Tikka et al. 2000), the sites within our neighbour pairs were mainly (in 37 out of 61 pairs) along different traffic routes. We thus claim that spatial autocorrelation of properties related to the surrounding environment or traffic routes themselves is not an underlying reason for the similarity of vegetation at neighbouring sites.

Occurrence of the same grassland species at neighbouring sites does not guarantee that these species really move along road and railway corridors instead of using the shortest route across the matrix habitat. The effect of the surrounding environment on species composition of road and railway sides (Stottele 1994; Tikka et al. 2000) indicates that plants are able to spread to verges from the adjacent areas. Therefore it appears logical to assume that dispersal could take place from verges to surroundings as well. This is, however, improbable for the grassland species studied here, since the most common matrix environment in Finland consists of forested areas (Sevola 1997), and the majority of the sites were separated by coniferous forests. Grassland species requiring open, moderately disturbed habitats are unlikely able to colonise new areas by proceeding through forests that are inhospitable habitats with closed canopies and acidic soils. The probability of long leaps through forests is further diminished by the relatively poor dispersal ability of many grassland species (Table 1). One-third of the species studied here has adaptations for dispersal by animals and can potentially be transferred even across forests. Small mammals, for instance, are known to switch between roadside ditches and other habitat types (Cummins and Vessey 1994). In Finland, however, the role of animals in seed dispersal on verges is largely unknown. The seeds of species that lack specialised mechanisms for dispersal drop in the vicinity of parent plant and therefore need suitable patches for germination nearby (Willson et al. 1990; van Dorp 1996). The seeds of wind-dispersed grassland species need high quality patches as well and rarely survive if deposited in a forest. Consequently, road and railway verges constitute the most probable route for dispersal of grassland plants.

Even though natural dispersion of grassland species that lack specialised dispersal mechanisms is slow, it may be differently assisted on road and railway verges. The equipment used for haymaking transport seeds in agricultural areas (Strykstra et al. 1997). Similarly, seeds of plants growing on road and railway verges are obviously carried along by machinery used for mowing the embankments. Seeds of several species have also been observed to travel attached to cars and trains, and even establishments of new populations as a result have been reported (Schmidt 1989; Ernst 1998).

In this paper we introduced a novel method for assessing dispersal (or, spatial association in general) of a large group of species. Although the results strongly point to the conclusion that grassland plants use road and railway verges as dispersal corridors, our data were not initially collected for a study of this kind. An experimental design and data sampling planned especially for this approach would be favourable to exclude sources of systematic error such as spatial autocorrelation. Different approaches to study the role of corridors have been presented in the literature (e.g., Nicholls and Margules 1991; see also Inglis and Underwood 1992) but unfortunately they are not applicable here. One possible design for our approach is as follows. For each study site two reference sites, a 'roadside neighbour' and a 'matrix neighbour' serving as a control, are chosen. The roadside neighbour is a site having a direct road connection to the study site. The matrix neighbour is a site situated at the same distance to the study site (measured through the matrix) as the roadside neighbour, but which is markedly farther from the study site measured along roads.

Although the sampling design of our data was not optimal in regards of assessment of dispersal, the result supporting the corridor hypothesis is encouraging. As the disappearance of semi-natural grasslands and other open, cultural habitats is the main reason for the threatened status for 31% of the threatened vascular plant species in Finland (Rassi et al. 2000), the ability of road and railway verges to serve as substitute habitats and dispersal routes is an important feature in preservation of grassland plant populations. If the decline of semi-natural grasslands continues, capability to live in and disperse along traffic route corridors may become essential for persistence of many species. A few roadside spots having high floristic values are already managed with special care, but a broader application of natural management methods would

surely further promote the occurrence and dispersal of grassland species on road and railway verges.

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### Appendix 1.

Since exact calculation of the expected numbers of same species growing at two sites, under spatial randomness and given the true numbers of species growing at the sites, would have been far too complicated, the following approximation was applied. The probability that an arbitrary species  $i$  grows at an arbitrary site  $S$  having  $s$  species is approximated as

$$P(i \in S|s) \approx 1 - \prod_{k=0}^{s-1} \left( 1 - \frac{n_i}{\sum_{j=1}^I n_j - k\bar{n}} \right),$$

where  $P(i \in S|s)$  is the probability that species  $i$  grows at site  $S$  given that there are  $s$  species in  $S$ ,  $n_i$  is the number of sites in the data having the species  $i$ ,  $I = 67$  is the total number of species in the data and  $\bar{n} = (\sum_{i=1}^I n_i) = 3.25$  is the average number of sites inhabited by an arbitrary species. The symbol  $\prod$  stands for a product of terms,  $\prod_{i=1}^n a_i = a_1 a_2 \dots a_n$ .

In a spatially random case, the probability that a species  $i$  occurs at two (neighbouring) sites  $S$  and  $T$  (having  $t$  species) is simply  $P(i \in S|s)P(i \in T|t)$ . Hence, the expectation of the number  $b_{st}$  of species growing at both sites, given the true numbers there, can be estimated by summing over all species,

$$\mathbf{E}(b_{st}|s, t) \approx \sum_{i=1}^I \left[ 1 - \prod_{k=0}^{s-1} \left( 1 - \frac{n_i}{\sum n_j - k\bar{n}} \right) \right] \left[ 1 - \prod_{k=0}^{t-1} \left( 1 - \frac{n_i}{\sum n_j - k\bar{n}} \right) \right].$$

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