

ASSESSING THE RELATIVE IMPORTANCE OF DISPERSAL IN PLANT COMMUNITIES USING AN ECOINFORMATICS APPROACH

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Abstract: Increased insight into the factors that determine the importance of dispersal limitation on species richness and species composition is of paramount importance for conservation and restoration ecology. One way to explore the importance of dispersal limitation is to use seed-sowing experiments, but these do not enable the screening of large sets of species and habitats. In the present paper we present a complementary approach based on comparing small plots with larger regions with regard to species composition and distribution of functional traits. We developed a GIS tool based on ecological and geographical criteria to quantify species pools at various spatial scales. In this GIS tool, containing floristic, large databases, phytosociological and functional information are exploited. Our premise is that differences in the nature of the species in local and regional species pools with regard to functional traits can give important clues to the processes at work in the assembly of communities.

We illustrate the approach with a case study for mesotrophic hay meadows (*Calthion palustris*). We tested the effects of differences in frequency in the local Habitat Species Pool and differences in dispersal and persistence traits of species on local species composition. Our results show that both species pool effects and functional traits affect the probability of occurrence in small plots. Species with a high propagule weight have, given the frequency in the Local Habitat Species Pool, a lower probability of occurrence in small plots. The probability of local occurrence, however, is increased by the ability to form a persistent soil seed bank and by adult longevity. This provides support for the view that the degree of dispersal limitation is dependent on the degree of spatial isolation of the focal site relative to source populations and moreover that species inherently differ in the degree to which dispersal limitation is a limiting factor for local occurrence.

Keywords: Community assembly, Dispersal limitation, Ecoinformatics, Functional traits, Spatial isolation, Species pool

INTRODUCTION

Evidence is accumulating that local species richness and species composition is determined by both niche based processes and dispersal processes (RICKLEFS & SCHLUTER 1993, ZOBEL 1997, GRACE 1999, KUPFERSCHMID et al. 2000, GRIME 2001, XIONG et al. 2003, FOSTER et al. 2004, OZINGA et al. 2005). However, knowledge of the relative importance of both sets of processes under various conditions is fragmentary (HUSTON 1999, KOLB & DIEKMANN 2004, MOUQUET et al. 2004, ZOBEL & KALAMEES 2005). From a theoretical perspective, this knowledge is important since it touches upon basic principles of community assembly.

Increased insight into the factors that determine the relative importance of various constraints on species richness and species composition is also of paramount importance for conservation and restoration ecology. Growing concern about the decrease of biodiversity at local and regional scales has resulted in increased efforts for restoration of species rich habitats. Even if abiotic conditions can be restored sufficiently, the degree to which characteristic species recolonize the target area is often disappointing (e.g. HUTCHINGS & BOOTH 1996, BAKKER & BERENDSE 1999, LOCKWOOD & PIMM 1999). It is increasingly acknowledged that the availability of seeds can be a major limiting factor in ecological restoration projects (BAKKER & BERENDSE 1999, TURNBULL et al. 2000, EHRLÉN & ERIKSSON 2000, MOUQUET et al. 2004). For efficient restoration efforts it is therefore important to have reliable indications to what degree the lack of certain target species might be explained by dispersal limitation or whether other constraints are involved. In other words: it is necessary to differentiate between sites that are unsuitable for the establishment of species from an environmental perspective and sites that are suitable but yet unoccupied (FRECKLETON & WATKINSON 2002, MÜNZBERGOVÁ & HERBEN 2004, OZINGA et al. 2005).

HOW TO TEST THE RELATIVE IMPORTANCE OF DISPERSAL

Seed addition experiments

One way to explore the relative importance of dispersal limitation is the use of seed-sowing experiments (e.g. TILMAN 1997, TURNBULL et al. 2000, ZOBEL et al. 2000, XIONG et al. 2003, MOUQUET et al. 2004). If sowing plant species from the regional species pool results in a sustainable increase in species number at the local scale, we may take this as evidence that species richness is limited by dispersal (FOSTER & TILMAN 2003, ZOBEL & KALAMEES 2005). Seed addition experiments however suffer from several methodological complications (MOUQUET et al. 2004, ZOBEL & KALAMEES 2005) and we agree with Zobel & Kalamees that there is a need for well designed, long-term seed addition experiments according to a common design across various ecosystems and geographical regions. However, there is a dilemma between scale and precision. A large-scale experiment may differentiate between alternative hypotheses on the importance of dispersal limitation, but it does not enable the screening of large sets of species and habitats. This is an important drawback from the perspective of restoration ecology, because information on the degree of dispersal limitation is needed for large sets of species and habitats. This dilemma between scale and precision of ecological research may be mitigated by adopting complementary approaches.

Analyses of species richness across spatial scales

Early attempts to deduce the importance of dispersal limitation were based on simple correlations between local and regional species numbers for a given habitat type (e.g. RICKLEFS 1987, CORNELL 1993, PÄRTEL et al. 1996, ZOBEL 2001). The critical issue in these studies was whether (1) local species richness “saturates” at some level independent of the total size of the pool of regionally available species, or (2) local species richness continues to increase as the size of the regional species pool increases. In the first case species richness is considered to be controlled by local interactions, while in the second case local species richness is mainly controlled by regional processes (CORNELL 1993, HUSTON 1999). Using a meta-analysis CORNELL & KARLSON (1997) and CORNELL (1999) showed that unsaturated species-richness curves are the rule, thus supporting the view that dispersal limitation is an important constraint for local species richness.

Correlations between local species richness and the size of the regional species pool, however, cannot exclude the possibility that these relations are simply a passive result of the accumulation of local processes (ROSENZWEIG & ZIV 1999, HERBEN 2000, LEPS 2001, WILSON & ANDERSON 2001). Moreover this approach may suffer from the inclusion of inappropriate spatial or temporal scales with regard to the processes of interest (HUSTON 1999). In several studies (e.g. in CORNELL & KARLSON 1997) the scale of local plots was too large in comparison to the scale at which interspecific interactions take place (HUSTON 1999, LOREAU 2000).

Analyses of species composition and functional traits across spatial scales

A possible way to overcome the methodological problems associated with the comparison of the species numbers across spatial scales may be to shift the focus from species numbers towards the composition and functional attributes of the species concerned. In this paper we propose the use of such an approach based on the linkage of information available in large databases. Our premise is that differences in the nature of the species in local and regional species pools with regard to functional traits, can give important clues to the processes at work in the assembly of communities. Dispersal limitation is expected to be affected by processes at both the landscape level and the species level.

At the landscape level, the degree of dispersal limitation can be affected by the composition and frequency of species in the species pool, since this determines the availability of propagules.

At the species level there are intrinsic differences in the ability to disperse in space and through time, due to trade-offs between dispersal ability and other life-history traits. Dispersal ability is hypothesized to be negatively related to adult longevity and competitive ability (GRUBB et al. 1982, VENABLE & BROWN 1988, TILMAN 1994, EHRLÉN & VAN GROENENDAEL 1998) or to the ability to establish under harsh conditions (GRIME & JEFFREY 1965, WESTOBY et al. 1996, LEISHMAN 1999). In metapopulation theory, the probability of local occurrence of species is described as a dynamic equilibrium between colonization and local extinction (HANSKI 1998, HANSKI & GAGGIOTTI 2004). Traits affecting species' dispersal ability and local persistence can be expected to affect this equilibrium (TILMAN

1994, EHRLÉN & VAN GROENENDAEL 1998, ERIKSSON 2000). The degree of dispersal limitation may therefore be expected to differ between species.

Although the existence of interspecific differences in dispersal traits is well established, this does not necessarily mean that these differences at the species level affect local species composition. This is only the case if dispersal limitation is an important process relative to other processes that determine local species composition such as resource availability and species interactions. HUBBELL (2001) even suggests that interspecific differences in traits are not important at all in determining patterns in species regional abundance (frequency). HUBBELL (2001) explains abundance patterns solely based on random processes. The critical question is thus not whether species differ in their dispersal ability, but whether these differences translate into differences in the probability of local occurrence. In the present paper we tested the effects of differences in frequency in the species pool (landscape level) and differences in dispersal traits (species level) on local species composition. In the case study we tested the following hypotheses:

Landscape level

H0: The probability of occurrence of species in small plots is independent of the frequency of species in the species pool.

H1: The probability of occurrence of species in small plots increases with frequency in the species pool.

Species level

H0: No differences exist between species with different functional traits in their probability of occurrence in small plots, given their frequency in the species pool.

H1: Species with a limited ability for dispersal in space, for dispersal through time or with a short adult longevity are under-represented in small plots, given their frequency in the species pool.

INTRODUCTION OF AN ECOINFORMATICS APPROACH

Outline of the approach

In the present paper we present an approach for the quantification of the relative importance of dispersal limitation based on a comparison of small plots with larger regions with regard to species composition and distribution of functional traits. For this comparison we used large databases containing spatiotemporal data on species composition in small plots (< 100 m²) as well as species occurrences in 1 km² grid cells. The third component of our approach consists of a species trait database containing information on the capacity of species to disperse in space and through time and on adult lifespan. The databases were applied within a Geographic Information System (GIS) to determine the species composition and functional attributes on different spatial scales. The integration of vast ecological databases on different organisational levels and across spatial scales to reveal new information can be regarded as an example of the emerging field of “ecoinformatics”.

The databases

Vegetation database

Co-occurrence data were obtained from the vegetation database of the Netherlands, which comprises over 400,000 specific descriptions of the species composition of small plots (HENNEKENS & SCHAMINÉE 2001). It probably is the largest database of local plant species co-occurrence data worldwide to date. The database is based on a large “space-time window” (plots having been described throughout the Netherlands from 1930 to 2000) and covers a large proportion of the environmental “niche space” in the Netherlands. Plot size in this database has been scaled approximately according to the mean size of individual plants and ranges from 4 m² (grasslands) to 100 m² (forests). The position of all plots is recorded within a 1 km² grid (and often the exact coordinates are given as well).

Floristic databases

Floristic data were obtained from the databases FLORIVON and FlorBase. For further details see VAN DER MEIJDEN et al. (2000) and TAMIS & VAN 'T ZELFDE (2003). These databases contain information on species occurrences within 1 km² grid cells in the Netherlands from 1902–1949 and from 1975–1999, with 1.7 million respectively 4.3 million records. In the present paper we only used the recent floristic data.

Functional trait database

Data on functional traits of species were extracted from the IRIS database on life-history traits of the species of the Dutch flora (www.synbiosys.Alterra.nl/IRIS). The IRIS database includes three groups of traits that are considered to be important for the spatial and temporal dynamics of species (cf. TILMAN 1994, ERIKSSON 2000, EHRLÉN & VAN GROENENDAEL 1998): (1) potential for long-distance dispersal, (2) potential to build up a persistent soil seed bank (“dispersal through time”), and (3) adult persistence (see Table 1). These three traits are expected to contribute to the predictability of the local occurrence of a particular species, either by fast and frequent recolonization of unoccupied sites or by persistence once a recolonization has taken place.

For dispersal in space we consider the following dispersal vectors with a high efficiency for long-distance dispersal: water (hydrochory), wind (anemochory), attachment to the fur of large mammals (epizoochory by mammals), survival in the digestive tract of large mammals (endozoochory by mammals) and frugivorous birds (endozoochory by birds). In order to include as many species as possible and to facilitate comparisons between different dispersal vectors, we aggregated the available data into a binary classification, assigning each species to one of two classes for each dispersal agent: “1” if the species has attributes that give access to a given vector and “0” if the species has no such attributes (see OZINGA et al. 2004). Although the binary classification of the continuum is less precise for the individual case, it allows generalizations at the level of large species pools. For the classification of dispersal through time we used the seed longevity index (after BEKKER et al. 1998, based on THOMPSON et al. 1997) that is included in the IRIS database. Species were classified as long-lived if their lifespan exceeds two years.

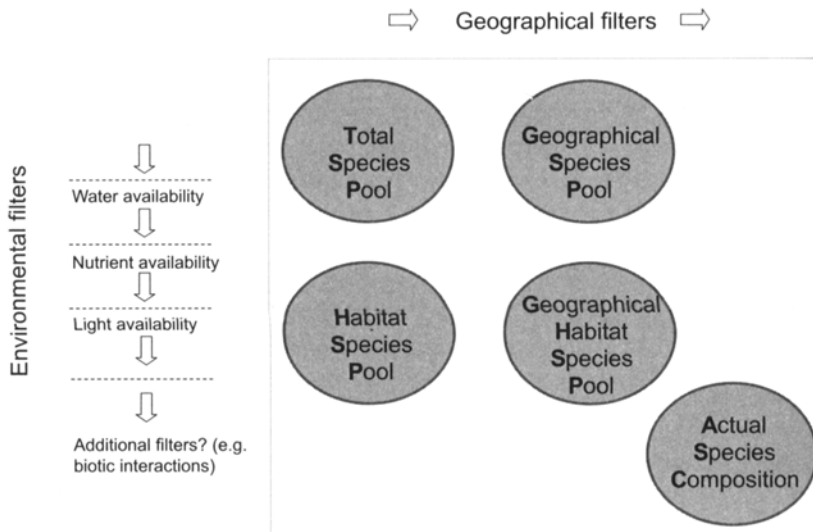


Fig. 1. Conceptual model of the major constraints on the composition of the actual species composition in small plots, which operate as environmental filters and isolation filters on the Total Species Pool. The Geographical Species Pool can be determined at various spatial scales (e.g. local versus regional sensu ZOBEL 1997). Terminology for species pools adopted from KELT et al. 1995, terminology of filters is adapted from KEDDY (1992) and ZOBEL (1997), while the nature of the environmental filters is based on OZINGA et al. (2005).

The determination of species pools from the databases

In this paper we follow ERIKSSON (1993) and ZOBEL (1997) in defining the species pool as a set of species that are potentially capable of coexisting in a certain community. This concept thus implies that for an ecologically relevant estimation of species pools both habitat tolerances (environmental filter) and the spatial distribution (geographical filter) of species must be known (ZOBEL 1997, ZOBEL et al. 1998). Within a GIS-environment we developed a “species pool tool” that uses both criteria to quantify the species composition of various species pools from the total species list. A conceptual overview of our approach is given in Fig. 1.

Environmental filters

The assembly of local communities is governed by processes that act like filters to select community members from the broader species pool (e.g. KEDDY 1992, ZOBEL et al. 1998, GRIME 2001). Such ecological filters applied to the Total Species Pool (TSP) results in a Habitat specific Species Pool (HSP, sensu KELT et al. 1995, see Fig. 1). HSP’s can be defined using detailed knowledge of the optimal occurrence and tolerances of species along the major environmental gradients (KEDDY 1992, ZOBEL et al. 1998). Alternatively HSP’s can be defined using a hierarchical classification of plant communities (phytosociological approach cf. ZOBEL et al. 1998, DUPRÉ 2000). This approach builds on the premise that the set of species that are present in a plot has a predictive value for the habitat suitability of that plot for other species that are not present (cf. MCCUNE 1994, WITTE 1998, EWALD 2002). Each individual plot was assigned to one or more vegetation types (maximal three) using the software package ASSOCIA (VAN TONGEREN 2004). The assignment of each plot is based on

the calculated maximum likelihood, using the dissimilarity between a plot and a set of pre-classified reference plots. All species that were observed with a frequency of more than one percent within a plant community were assigned to the HSP of that community. For plots that were identified as transitions between two or three vegetation types we used for each species the average for the frequency values in the vegetation types weighted by the likelihood for the assignment to each vegetation type. The HSP can be regarded as a “fuzzy set” composed of species with a different degree of community membership and most species belonging to more than one HSP. Note that HSP’s are scale independent and constitute habitat defined subsets of the Total Species Pool (TSP).

Geographical filters

Based on the spatially explicit floristic inventories of 1 km² grid cells in the Netherlands it is possible to quantify the species composition of a Geographically delimited Species Pool (GSP sensu KELT et al. 1995) at several spatial scales. On the largest spatial scale the GSP_{Netherlands} equals the Total Species Pool and is defined as the total species list for the Netherlands with their frequencies based on the floristic databases (number of occupied 1 km² grid-cells; VAN DER MEIJDEN et al. 2000).

At smaller spatial scales it is possible to quantify the species composition in the surroundings of any specific locality in the Netherlands. We used the GIS package ArcView GIS 3.2 (ESRI Inc. 1999) to quantify the percentage of occupied 1 km² grid cells in circles around each selected plot at various spatial scales. This results in a series of local and regional Geographical Species Pools (GSP) for each plot. The spatial scales can be user defined by specifying the radius around the focal locality.

Geographical and ecological filters combined

Since species pools make sense only for sets of species that are potentially capable of coexisting in a certain community, we filter the GSP with the species list from the HSP. This Geographically delimited Habitat Species Pool (GHSP) is thus the site specific and scale specific intersection of HSP and GSP (e.g. $\text{GHSP}_{r=3 \text{ km}} = \text{HSP} \cap \text{GSP}_{r=3 \text{ km}}$). GHSP’s are unique for each plot for each spatial scale. Higher frequency values in the local and regional GHSP are regarded as indicative for a higher probability of propagule dispersal towards the focal plot, and hence indicate a lower degree of isolation of the focal site. The user defined scale in the GHSP enables a flexible quantification of the composition and frequency distribution of species across spatial scales.

QUANTIFICATION OF THE RELATIVE IMPORTANCE OF DISPERSAL: A CASE STUDY

Materials and methods

In order to illustrate our approach we present the results of a case study from one plant community. We selected moist mesotrophic hay meadows belonging to the association *Ranunculo-Senecionetum aquatici* (alliance *Calthion palustris*) as described in SCHAMINÉE et al. (1995–1999). The ecology of this community is well studied in the Netherlands (e.g. EVERTS & DE VRIES 1991, BAKKER & OLFF 1995, SCHAMINÉE et al. 1995–1999,

Table 1. Overview of the functional plant traits used in the case study.

Functional trait	Description
GHSP _{Netherlands}	Number of occupied 1 km ² grid cells in the period 1975–1999 (log transformed)
GHSP _{r=3 km}	Percentage of occupied 1 km ² grid cells within a radius of 3 km around the focal plot
Propagule weight	Propagule weight (mg; log transformed)
Dispersal potential water	Potential for Long Distance Dispersal by water (0 = low, 1 = high)
Dispersal potential wind	Potential for Long Distance Dispersal by wind (0 = low, 1 = high)
Dispersal potential fur	Potential for Long Distance Dispersal by fur of mammals (0 = low, 1 = high)
Dispersal potential dung	Potential for Long Distance Dispersal by dung of mammals (0 = low, 1 = high)
Dispersal potential birds	Potential for Long Distance Dispersal by bird-droppings (0 = low, 1 = high)
Seed longevity	Persistence in the soil seed bank (classified with the Seed Longevity Index ranging from 0 = low to 1 = high)
Adult longevity	The average length of life of an adult plant (1 = annual or biennial, 2 = perennial)

GROOTJANS et al. 1996). The composition of the Habitat Species Pool (HSP) for this plant community was derived from SCHAMINÉE et al. (1995–1999), but the frequency of the constituting species was derived from the floristic database (GHSP_{Netherlands} = HSP ∩ GSP_{Netherlands}).

We used a selection of 500 plots, each with an area of 4 m² for which the position within the 1 km² grid is known. Each 1 km² grid cell was represented maximally by one plot, and plots are scattered throughout the Netherlands to reduce confounding effects of spatial autocorrelation. For each plot the actual occurrence of all the species of the GHSP_{Netherlands} was scored on a binary scale (present or absent). Subsequently, we determined the GHSP within a radius of 3 km (GHSP_{r=3 km}) for each plot. Although the determination of species pool effects across spatial scales is possible with this GIS approach, this is beyond the illustrative scope of the present case study. The (GHSP_{r=3 km}) is based on floristic information from maximally 45 km² grid cells. Plots near the Dutch border were excluded. For the determination of GHSP_{r=3 km} we only used the recent floristic data. The set of plot specific species pools can now be used to test the hypothesis that frequency in the species pool (GHSP_{r=3 km}) is a good predictor of occurrence in the small plots.

After this, the results can also be linked to the database with functional traits to test for additional effects of functional traits on the probability of occurrence in the 4 m² plots. An overview of the functional traits included in the present study is provided in Table 1.

Statistics

The relative importance of spatial isolation and various functional traits on the probability of occurrence in small plots was quantified by means of multiple logistic regression. This method is based on fewer assumptions than simple linear regression (MCCULLAGH & NELDER 1989) and is considered an effective method in describing binary ecological data (e.g. AUSTIN et al. 1990, TREXLER & TRAVIS 1993, HUISMAN et al. 1993). Although high proportions of unexplained variance are inherent to presence / absence data since the chance of occurrence in specific sites translates into a binary pattern, logistic regression may still provide a powerful tool to separate between alternative hypotheses (AUSTIN et al. 1990,

Table 2. Results of multiple logistic regression with the probability of occurrence in 4 m² plots as dependent variable and the frequency of occurrence in the GHSP and functional traits as independent variables. Wald statistics are a measure of the relative effect size of the variables in the full model. Deviations of the odds ratios from 1 indicate the increase in site occupancy with the increase of a given variable. Nagelkerke's R² gives the cumulative proportion of explained variance after entrance of the variable.

Variable	Wald	d.f.	Sig.	Odds ratio	Nagelkerke R ²
Null model					
GHSP _{Netherlands}	130.789	1	< 0.001	1.182	0.004
Species pool effect					
GHSP _{r=3 km}	3285.395	1	< 0.001	1.034	0.190
Functional traits					
Propagule weight	88.492	1	< 0.001	0.816	0.204
Dispersal potential water	423.169	1	< 0.001	0.505	0.215
Dispersal potential birds	92.641	1	< 0.001	0.205	0.219
Adult longevity	216.156	1	< 0.001	1.639	0.223
Seed longevity	137.216	1	< 0.001	1.799	0.227
Dispersal potential fur	87.567	1	< 0.001	1.423	0.230
Dispersal potential wind	85.032	1	< 0.001	1.447	0.233
Dispersal potential dung	28.308	1	< 0.001	0.852	0.234
Constant	3806.911	1	< 0.001	0.010	

TREXLER & TRAVIS 1993). The statistical analyses were performed using SPSS 10 (SPSS Inc. 1999).

As individual cases we used the occurrence of a given species in a given plot (0 or 1) and associated to this record the percentage of occupied 1 km² grid cells within a radius of 3 km (plot and species specific). The total number of cases was 36,295.

In order to test for the effects of species frequency in the local GHSP we need a proper null model based on random dispersal. For a given habitat random dispersal would imply that the species were assigned to plots by a weighted lottery (cf. CHESSON & WARNER 1981) in which the probability of occurrence in a plot is determined by the frequency in the GHSP_{Netherlands}. Therefore we used a regression model with the percentage of occupied 1 km² grid cells (log transformed) in the Netherlands (GHSP_{Netherlands}) as our null model for each species, and this variable was entered first into the regression model.

We performed the multiple logistic regression in three steps. Firstly, we tested the effect of abundance in the GHSP for the entire Netherlands (GHSP_{Netherlands}). This model was used as our null model. Secondly, we tested for the effect of spatial isolation relative to the null model, and thirdly we tested for additional effects of functional traits. In the third step the functional traits were entered in the model by stepwise forward selection. The parameters of the model were estimated by the likelihood ratio test. This is an assessment of the improvement of the fit between the predicted and observed values on the response variable by adding the predictor variable. Only variables for which the likelihood ratio χ^2 had a *P*-value < 0.05 were included in the model.

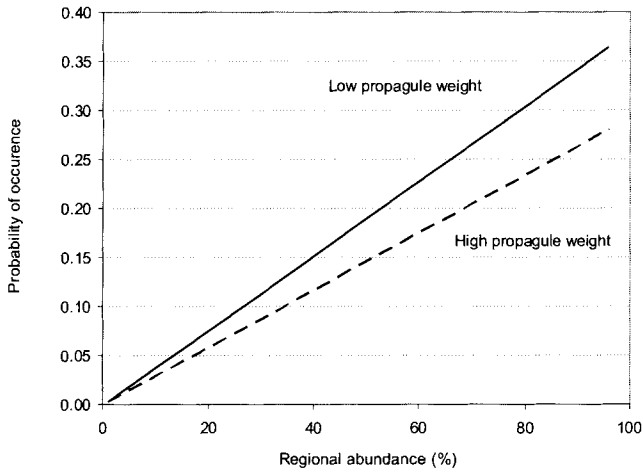


Fig. 2. Relation between probability of occurrence of a species in a small plot and the frequency of the species in the Geographical delimited Habitat Species Pool (GHSP_{r=3 km}) for species with propagule weight < 0.3 mg and for species with propagule weight > 0.3 mg. The lines are based on fitted aggregated data (probability of occurrence within abundance classes with an interval of 1%).

RESULTS AND DISCUSSION

Our test of the hypotheses at the landscape level is presented in Table 2 (null model versus species pool effect). The results demonstrate that the frequency of species in the Habitat Species Pool for the entire Netherlands (GHSP_{Netherlands}) explains a significant proportion of the variation in probability of occurrence in small plots. This can be regarded as an effect of random sampling from the GHSP_{Netherlands} according to statistical rules without ecological meaning. This result is consistent with lottery theory (CHESSON & WARNER 1981) and with neutral theory (HUBBELL 2001), in which species are common or rare purely by chance. The proportion of explained variance, however, is very low (Nagelkerke $R^2 = 0.004$) indicating that this cannot be the main explanation for species occurrence patterns, and thus there must be other mechanisms involved in the assembly of local communities.

The inclusion of spatial differences in the frequency within the local Habitat Species Pool (GHSP_{r=3 km}) largely improves the performance of the model (Table 2; Nagelkerke $R^2 = 0.190$). The large effect of frequency in GHSP_{r=3 km} in explaining the actual occurrence in 4 m² plots is consistent with both species pool theory (ERIKSSON 1993, ZOBEL 1997) and metapopulation theory (HANSKI 1998, HANSKI & GAGGIOTTI 2004). High densities of propagules across the landscape increase the probability of colonization of unoccupied patches. Can recolonizations of already occupied patches buffer sites against local extinction (HANSKI 1998)?

The results at the species level indicate that the probability of local occurrence, given the frequency in the Local Habitat Species Pool (GHSP_{r=3 km}), is affected by functional traits (Table 2). The additive effect of functional traits is illustrated in Fig. 2 for propagule weight. Species with a high propagule weight have, given the frequency in the Local Habitat Species

Pool (GHSP_{r=3 km}), a lower probability of occurrence in small plots. This can be explained by a trade-off between seed mass and seed number (JAKOBSSON & ERIKSSON 2000, MOLES et al. 2004). The lower seed output of larger-seeded species means that they have a lower probability to reach suitable sites. Furthermore the probability of local occurrence is negatively correlated with the ability to disperse with water, mammals (internal) or with birds, although the effect size for these variables was limited. The negative correlations for these dispersal traits may be explained by changes in land use in the Netherlands during the 20th century (OZINGA et al., unpubl. data). The probability of local occurrence, however, is increased by the ability to form a persistent soil seed bank, by adult longevity and by the ability to disperse by wind or in the fur of mammals. The degree of dispersal limitation, given the frequency in the GHSP, will therefore differ between species according to their functional attributes.

CONCLUSION

Our results indicate that both species pool effects (spatial differences in the frequency of species in the local Habitat Species Pool) and functional traits related to dispersal and local persistence affect the probability of occurrence in small plots. This provides support for the view that degree of dispersal limitation is dependent on the degree of the focal site's spatial isolation relative to source populations and moreover that species inherently differ in the degree to which dispersal is a limiting factor for local occurrence.

These results have important implications for restoration ecology. In highly isolated target areas with an impoverished local Habitat Species Pool (GHSP_{r=3 km}) it will not be feasible to re-establish a representative subset of the total Habitat Species Pool (GHSP_{Netherlands}). Characteristic species that are rare in the local GHSP or that lack certain functional traits will be under-represented in comparison to historical references. This means that either the aims have to be adjusted or alternatively that additional measures are needed, such as reintroduction of species.

PERSPECTIVES FOR THE ECOINFORMATICS APPROACH

Our results illustrate that the linkage of databases with spatially explicit data and with functional data within a Geographical Information System can be a powerful tool in the assessment of the relative importance of dispersal limitation. The species pool tool outlined in this paper is however amendable in various ways. In order to robustly analyze spatial effects the tool should include advanced methods for correction for confounding effects of spatial autocorrelation in environmental conditions (e.g. LEGENDRE et al. 2002). Moreover the species pool tool can be extended by inclusion of spatial explicit information on actual land-use and land-use history. Actual land use may have a large impact on the realized dispersal of propagules from source populations towards target sites. In some habitats past land use may be an even more important predictor of present day species composition (e.g. POSCHLOD & BONN 1998, COUSINS et al. 2003, LINDBORG & ERIKSSON 2004, OZINGA et al., unpubl. data). This is probably especially true for species with a high adult persistence or with a persistent soil seedbank.

The extension of the ecoinformatics approach critically depends on the availability of ecological data. Since spatial data are often very noisy due to the large role of stochastic events (e.g. HERBEN & HARA 2003), large phytosociological and floristic databases are required to test hypotheses on community assembly. Moreover the information should be compiled according to common standards (see MUCINA et al. 2000, CHYTRÝ 2001, EWALD 2003), and should be spatially and temporally explicit. The phytosociological databases should be compatible with floristic databases and trait databases with regard to database structure and taxonomy to enable the determination of habitat species pools at various spatial scales. The fast increase in availability of ecological databases holds a promise for the near future. Once these databases are sufficiently filled, the ecoinformatics approach presented here may provide a useful tool for the further analyses of hypotheses regarding factors that influence the degree of dispersal limitation.

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