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# The assembly of local communities: Plants and birds in non-reclaimed mining sites

**Martin Brändle, Walter Durka, Harald Krug and Roland Brandl**

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We correlated percentage of occurrence (local occupancy) of 1069 plant species and 155 bird species across 16 non-reclaimed mining sites in a brown coal district of eastern Germany to regional range size and life history traits. To control for possible confounding effects of phylogeny we used a cross-species as well as a phylogenetically controlled approach. Although life history traits showed significant correlations to local occupancy in univariate analyses, hierarchical partitioning suggested that these variables were only of minor importance to explain local occupancy across non-reclaimed mining sites. The most robust and consistent relationship, however, was found between local occupancy and regional range size. A greater proportion of bird species than plant species from the available species pool colonized the mining sites, possibly due to the active search for suitable habitats by birds. Thus, although the two groups have different ways of colonizing a habitat, the general importance of regional distribution is the same. Overall, the results of our study underline the importance of regional patterns to understand local community composition.

*M. Brändle and R. Brandl, Dept of Animal Ecology, Univ. of Marburg, Karl von Frisch Str., D-35032 Marburg, Germany. – W. Durka (correspondence: walter.durka@halle.ufz.de), UFZ Centre for Environmental Research Leipzig-Halle Ltd., Dept of Community Ecology, Theodor-Lieser Str. 4, D-06120 Halle, Germany. – H. Krug, Naturförderungsgesellschaft "Ökologische Station" Borna-Birkenhain e.V., Am Lerchenberg, D-04552 Borna-Birkenhain, Germany.*

For countries with mining activities, the restoration of ecosystems on mined areas is a financial issue. Hence restoration by spontaneous colonization and subsequent succession is of considerable importance (Prach and Pyček 1994, Jochimsen 1996). Furthermore non-reclaimed mining sites are of interest to conservation biologists: 1) within mining sites a diverse array of substrates with special physicochemical properties and low levels of nutrients occur (Varela et al. 1993, Durka et al. 1997, Brändle et al. 2000). Hence, non-reclaimed mining sites provide habitats for specialized and therefore endangered species (e.g. Ratcliffe 1974, Bruns 1988, Bradshaw 1989, Durka et al. 1997, Geißler-Strobel et al. 1997, Brändle et al. 2000). 2) Usually mining sites are fairly large. Thus, non-reclaimed mining sites provide the opportunity to protect ecological processes. For example, outside the Alps non-reclaimed mining sites are the only areas with primary succession (e.g. Prach et al. 1997, Prach and Pyček 1999). In fact, the communities of non-reclaimed mining sites are the result of primary succession. With time, a complex spatial pattern of communities develops in correlation to the soil properties and disturbances. Thus, a crucial step in the assembly of the communities within non-reclaimed mining sites is colonization. Which traits characterize species that colonize non-reclaimed mining sites? Are colonizers only a random sample from the available pool of species (e.g. Whittaker et al. 1989, Rydin and Borgegård 1991, Blackburn and Gaston 2001)?

The prediction of colonization patterns from life history traits has a long standing history in ecology and biogeography (e.g. the r- and K-concept, MacArthur

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and Wilson 1967, Pianka 1970, Southwood 1977, but see Stearns 1992). Early stages of primary successions are supposed to be dominated by r-selected species, short lived, small sized species with numerous offspring (Grubb 1987). For plants, Grime (1979) developed the C-S-R model which was also used to explain patterns of colonisation and succession (Grime 1986, Prach and Pyček 1999). Are these concepts sufficient to understand the occurrence of species in non-reclaimed mining sites?

In the last two decades, it became increasingly apparent that range size and abundance at larger spatial scales predict the composition of communities on nested scales (Zobel 1992, Ricklefs and Schluter 1993). Of course, life history traits may determine range sizes of species at large scales, but range size may reflect additional processes not covered by life history traits. Although range sizes are rather well known for some central European taxa (e.g. plants: Benkert et al. 1996; birds: Nicolai 1993), few attempts have been made to use them to predict colonisation probability of species (e.g. Welk and Hoffmann 1998). In the present study we will compare traits of species within the pool of potential colonisers to the traits of species which successfully colonised non-reclaimed lignite mining sites in eastern Germany. We chose plants and birds since a) life history traits of these groups are well known in central Europe, b) both groups are often used as umbrella taxa in conservation biology and c) the two taxa have different dispersal strategies (see Harrison et al. 1992). While plants are dispersed passively, birds search actively for habitats (Wiens 1992). We explore the following set of hypotheses: 1) Abundant or widespread species or those able to use a variety of habitats are the more successful colonisers (the "niche-breadth hypothesis" sensu Brown 1984). This hypothesis predicts a positive correlation between occurrence of species across non-reclaimed lignite mining sites versus the range size or niche-breadth (e.g. Brown 1984, Hanski et al. 1993). 2) Fast population growth should allow species to become more abundant and thus more likely to colonise suitable places. Furthermore species with large population growth should be safeguard against local extinction. Consequently these species are able to occupy more places than others (Gaston 1988, Hanski et al. 1993, Holt et al. 1997, Duncan et al. 1999). Thus we expect a correlation between population growth and colonization. 3) Plant species which do not depend on mutualistic relationships (e.g. animal pollination) should have a higher probability to establish founder populations. Thus, self- and wind-pollination should be traits favoured during early succession (e.g. Grime 1986, Whittaker et al. 1989, Prach and Pyček 1999). 4) Plant colonization has been shown to be constrained by seed dispersal (e.g. Lichter 2000). Thus, dispersal mode should affect colonisation and wind dispersed species should be more common than species with other dispersal mechanisms.

## Materials and methods

### Study area

Our study was carried out on opencast, non-reclaimed lignite mining sites in the brown coal district south of Leipzig, Germany (Fig. 1). Extensive mining started in that area at the beginning of the 20th century. After the German reunification most of the mines were closed. As part of the restoration planning, several non-reclaimed mines were surveyed for habitats and species (Durka et al. 1997). Lignite mining sites are often fairly large (hundreds of ha; Table 1) with a considerable diversity of landscape elements (valleys, steep slopes, erosion channels and banks of soil). Substrates at the surface consist of tertiary or quaternary deposits with low levels of nutrients (nitrogen content below 0.17%). pH ranges from $<3$ to 7.5 (Durka et al. 1997). The age of sites ranges from 10 to 50 yr (Table 1). Due to landscape diversity and disturbances, many different successional plant communities may be found within mining sites. There is no seed bank in the soils and thus these communities established from colonizers from the surrounding agricultural and industrial areas.

### Sampling

We surveyed seven non-reclaimed lignite mines between 1993 and 1997. Additional data on nine sites were available from published and unpublished reports (Table 1). Plant data were species lists of spontaneously occurring plant species in 14 sites. For birds we recorded breeding pairs of species in 15 sites. For plants and birds we used the number of occupied mining sites for further analyses, henceforth called local occupancy.

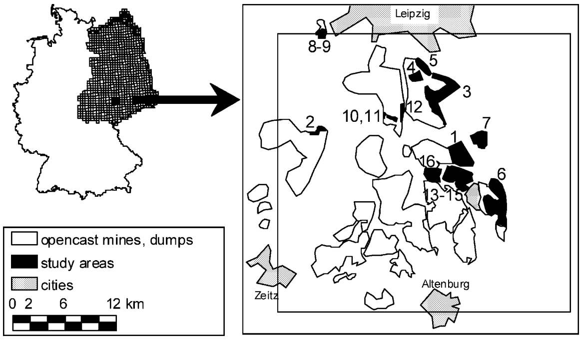


Fig. 1. Map of the study area. The left map informs about the location of the study area in Germany and the grid system to estimate regional range of plant and bird species. The right map indicates the distribution of the studied lignite mining sites south of the city of Leipzig. Site numbers correspond to those in Table 1. The area marked by the square was used to define the local species pool using the maps given in Nicolai (1993) and Benkert et al. (1996).

Table 1. Area, age, species richness of plants and birds within the 16 mining sites used during the present study. See also Fig. 1.

| | Site | Source of data (flora/avifauna) | Size (ha) | Age (yr) | Number of plant species | Number of breeding bird species |
|---|---|---|---|---|---|---|
| 1 | Restloch Haubitz | this study | 145 | 20 | 160 | 31 |
| 2 | Restloch Werben-Sittel | this study | 28 | 30 | 207 | 27 |
| 3 | Tagebau Espenhain | this study | 800 | 50 | 278 | 64 |
| 4 | Crostewitzer Höhe, Espenhain | this study | 300 | 20 | 136 | 26 |
| 5 | Espenhain Randschlauch Nord | this study (plant data only) | 100 | 20 | 227 | – |
| 6 | Tagebau Bockwitz/Borna-Ost | this study | 317 | 30 | 261 | 72 |
| 7 | Halde Trages | this study | 181 | 50 | 247 | 56 |
| 8 | Halde Kulkwitz-Forst | Dorsch and Dorsch 1988 | 21 | 30 | 130 | 37 |
| 9 | Halde Kulkwitz-Offenland | Dorsch and Dorsch 1988 | 32 | 30 | 94 | 25 |
| 10 | Tagebau Böhlen, Restloch 13 | Gutte 1993/this study | 15 | 50 | 207 | 43 |
| 11 | Kippenwald bei Zwenkau | Gutte 1993/this study | 115 | 40 | 285 | 49 |
| 12 | Spülkippe Lippendorf | Gutte 1993/this study | 20 | 20 | 203 | 34 |
| 13 | Altwitznitz-"Calamagrostis" | Kalbe 1958 | 10 | 10 | 18 | 6 |
| 14 | Altwitznitz-"Kahlschlag" | Kalbe 1958 | 8 | 10 | 16 | 10 |
| 15 | Altwitznitz-"Schonung" | Kalbe 1958 (bird data only) | 11 | 10 | – | 8 |
| 16 | Halde Witznitz | Rost 1981 (bird data only) | 9 | 10 | – | 29 |

## Potential colonizers and species traits

As the pool of potential colonizers we used all plant and bird species recorded in a 36 × 36 km area around the mining area (plants: Benkert et al. 1996; 1069 species; birds Nicolai 1993; 155 species). That is, we considered only species occurring in the neighbourhood of the mining sites which have therefore a chance to colonise. We refer to these species as the local species pool. Range size of plants was estimated as the number of 6 × 6 km grids out of the 3606 grids across eastern Germany (Benkert et al. 1996), for birds the range size was estimated by the number of 12 × 12 km grids out of 925 across eastern Germany (Nicolai 1993).

For plants and birds, we used the number of habitat types utilised by a species as a measure of habitat niche-breadth (plants: maximum = 24 habitat types: halophytic vegetation, dunes, rocks, alpine, ruderal vegetation, nitrophilous shrub, trampled sites, ruderal lawns, bogs, oligotrophic freshwater, eutrophic freshwater, periodically flooded sites, muddy soils, springs, moist grassland, meadows, heathland, dry grassland, xerothermic bushland, alpine bushland, moist forest, mesic broadleaf forest, acidic broadleaf forest, xerothermic woods; birds: maximum = 8 habitat types: salt-water, coastal land, heather land, rocks, hedges and woodland, moors and fens, farm land, urban areas; Table 2). In birds we also considered dietary niche-breadth, defined as the number of food categories exploited by a species (maximum = 22 categories, plants, water-plants, grasses, seeds, berries, insects, flying insects, water insects, soil living insects, spiders, slugs, worms, mussels, crustaceans, fishes, amphibians, reptiles, birds, eggs, mammals, carrion, others; Table 2; for further discussion about this measure of dietary niche breadth see Brändle et al. 2002a). Note that these categories also reflect the habitat types in which items occur. Maximum plant height was used as a quick and robust measure of competitive ability. In birds, we included several traits which are surrogates of population growth (Table 2: body size, clutch size, incubation time, fledging time, life span, number of clutches; see also Blackburn et al. 1996, Duncan et al. 1999). Since most of these variables were collinear, we performed a principal component analysis on a correlation matrix. The first component explained 44% of the total variance and could be interpreted as a gradient of population growth. Subsequent components accounted for only small proportions of variance and could not be interpreted in a straightforward way. Hence we used only the scores of species on the first component in subsequent analyses.

Dispersal and pollination traits of plants are based on Rothmaler (1990) and were taken from Frank and Klotz (1990). Types were ranked with increasing dispersal distance: self-dispersed (no morphological traits for any dispersal agent), ant-dispersed = 1; hydrochorous, epizoochorous = 2; endozoochorous = 3; anemochorous, human dispersed = 4. If more than one dispersal type was listed for a species, only the type with the highest rank was used. Pollination types were ranked with decreasing intensity of mutualistic interactions (insect pollinators, conspecific individuals): insect-pollinated = 1; insect + self-pollinated, water-pollinated = 2; wind-pollinated = 3; self-pollinated, apomictic, cleistogamous = 4. If more than one pollination type was listed for a species, only the type with the highest rank was considered.

## Phylogenetic analysis

Since species are not independent but linked by their evolutionary history it may be necessary to control for phylogenetic relatedness. Closely related species may share traits by common ancestry. Therefore, an analysis treating species as independent data points overestimates the degrees of freedom (Harvey and Pagel 1991). Recently, several approaches have been developed to tackle this problem (e.g. Felsenstein 1985, Grafen 1989, Pagel 1992, Purvis and Rambaut 1995). We used the method implemented in the CAIC package (Purvis and Rambaut 1995; see also Pagel 1992), which calculates phylogenetic independent contrasts across a phylogeny. In all analyses we applied the CRUNCH procedure which is the option to analyse continuous variables (Purvis and Rambaut 1995). Subsequently, relationships among contrasts were analysed using regression with an intercept of zero (Pagel 1992).

In order to construct a highly resolved plant phylogeny we used data from two sources: 1) phylogenies based on molecular data down to the family level and 2) within families traditional systematics based morphology but using molecular phylogenies when available (see Appendix 1). This resulting phylogeny allowed to calculate 676 contrasts across the 1069 species. To construct a phylogeny for the birds, we used the information given in Sibley and Ahlquist (1990). Although this phylogeny was criticized by various authors (e.g. Houde 1987, Sarich et al. 1989, Harshman 1994), it is currently the most comprehensive phylogeny available. This phylogeny produced up to 102 contrasts across the 155 species of the pool. In general we had no data to attach meaningful length estimates to all branches. Hence we were forced to set branch lengths as equal. This assumes a punctual evolution (Purvis and Rambaut 1995).

The random walk model ( = Brownian motion, Felsenstein 1985), which underpins our phylogenetically controlled analyses, assumes the same proportional change along each branch. Hence magnitude and sign of the standardised contrast should be independent of the estimated value of the character at the node of the phylogenetic tree at which the contrast was taken (Purvis and Rambaut 1995). We checked this for all variables by regressing the contrasts against the estimated nodal values (Purvis and Rambaut 1995). In some few cases we found significant relationships (e.g. contrasts of local occupancy in plants). Thus, the random walk model is not strictly valid.

## Statistical analysis

Analyses were performed using species as independent data points (cross-species approach) as well as using phylogenetic independent contrasts (PICs). We used local occupancy (see above) as dependent variable. In a first step, all traits were correlated to the dependent variables. Significance was assumed when type I error probabilities were $< 5\%$ (two-tailed). In a second step, we applied hierarchical partitioning, a recently developed technique related to multiple regression (Chevan and Sutherland 1991, MacNally 2000). The aim of hierarchical partitioning is not to identify a single optimal regression or a predictive equation. Rather all possible regression models are evaluated to estimate the average independent effect of a given independent variable on a dependent variable (MacNally 2000). This technique converts antagonistic effects into negative joint contributions effectively unmasking the indepen-

Table 2. List of independent variables used to explain local occupancy of plant and bird species across non-reclaimed lignite mining sites. References: [1] Benkert et al. (1996), [2] Anon. (1997), [3] Frank and Klotz (1990), [4] Nicolai (1993), [5] Korneck and Sukopp (1988); [6] Rothmaler (1990).

| independent variables | transformation | Categories |
|---|---|---|
| plants | | |
| regional range size [1] | arcsine$\sqrt{\%}$ | % 6 × 6 km grids occupied out of 3606 |
| habitat niche-breadth [5] | arcsine$\sqrt{\%}$ | % habitat types occupied out of 24 |
| dispersal types [3, 6] | – | 4 ranks according to increasing potential dispersal distance (see Methods) |
| maximum height [6] | $\log_{10}$ | maximal height (cm) |
| pollination types [3, 6] | – | 4 ranks according to increasing dependence on biotic interactions (see Methods) |
| birds | | |
| regional range size [4] | arcsine$\sqrt{\%}$ | % 12 × 12 km grids occupied out of 925 |
| habitat niche-breadth [2] | arcsine$\sqrt{\%}$ | % habitat types occupied out of 8 |
| dietary niche-breadth [2] | arcsine$\sqrt{\%}$ | % dietary categories exploited out of 22 |
| body size [2] | $\log_{10}$ | mean body size (in g) of male and female |
| clutch size [2] | $\log_{10}$ | maximal number of eggs per clutch |
| incubation time [2] | $\log_{10}$ | days of incubation |
| fledging time [2] | $\log_{10}$ | days of fledging |
| life span [2] | $\log_{10}$ | maximal age |
| number of clutches [2] | – | maximal number of clutches per year |

Table 3. Pearson correlation coefficient, r, and error probabilities, p, of arcsine square root transformed local occupancy of plants and birds across non-reclaimed lignite mining sites versus various independent variables. The results of the cross-species analysis ($r_{raw}$) and the phylogenetically controlled analysis ($r_{con}$) are shown. For further details of independent variables see Table 2. Bold numbers indicate significant correlation coefficients. Note that regressions among contrasts were calculated with an intercept of zero.

| independent variables | cross-species | | | phylogenetic independent contrasts | | |
|---|---|---|---|---|---|---|
| | n | $r_{raw}$ | p | n | $r_{con}$ | p |
| Plants | | | | | | |
| regional range size | 1069 | **0.69** | **<0.001** | 676 | **0.77** | **<0.001** |
| habitat niche-breadth | 1069 | **0.26** | **<0.001** | 676 | **0.35** | **<0.001** |
| dispersal types | 1069 | **0.10** | **<0.001** | 676 | 0.01 | 0.751 |
| maximum height | 1069 | **0.19** | **<0.001** | 676 | **0.20** | **<0.001** |
| pollination types | 1069 | −0.04 | 0.232 | 676 | −0.06 | 0.096 |
| Birds | | | | | | |
| regional range size | 155 | **0.60** | **<0.001** | 102 | **0.62** | **<0.001** |
| habitat niche-breadth | 155 | **0.17** | **0.034** | 102 | **0.30** | **0.002** |
| dietary niche-breadth | 155 | −0.11 | 0.191 | 102 | **0.24** | **0.030** |
| population growth | 124 | **0.41** | **<0.001** | 87 | 0.04 | 0.74 |

dent contributions which can be larger than the univariate squared partial correlation (Chevan and Sutherland 1991). To asses statistical significance of independent contributions we used randomisations (99 randomisations). We considered independent contributions as significant if five or less percent of the randomisations generated contributions equal or larger than the contribution calculated from the original data.

Copies of the data as well as of the phylogeny used during the present study are available on request.

## Results

### Plants

In total 549 plant species were recorded across all sampled mining sites (mean = 176 ± 88 SD, range: 16–285). Thus 51% of the local species pool was found within the mining sites. The univariate analyses with species as independent data points revealed that four out of the five traits were significantly correlated to local occupancy (Table 3): Species having a large local occupancy across non-reclaimed lignite mining sites are widely distributed on the regional scale, do occupy a large range of habitats, have an efficient dispersal mechanism and are tall. The phylogenetically controlled univariate analysis corroborated these findings (Table 3). The results of the hierarchical partitioning of the raw data (Fig. 2, upper left) and the phylogentical independent contrasts (Fig. 2, upper right) were very similar. Except of pollination type, most independent variables explained a significant part of variance. Nevertheless the most important independent variable was regional range size.

### Birds

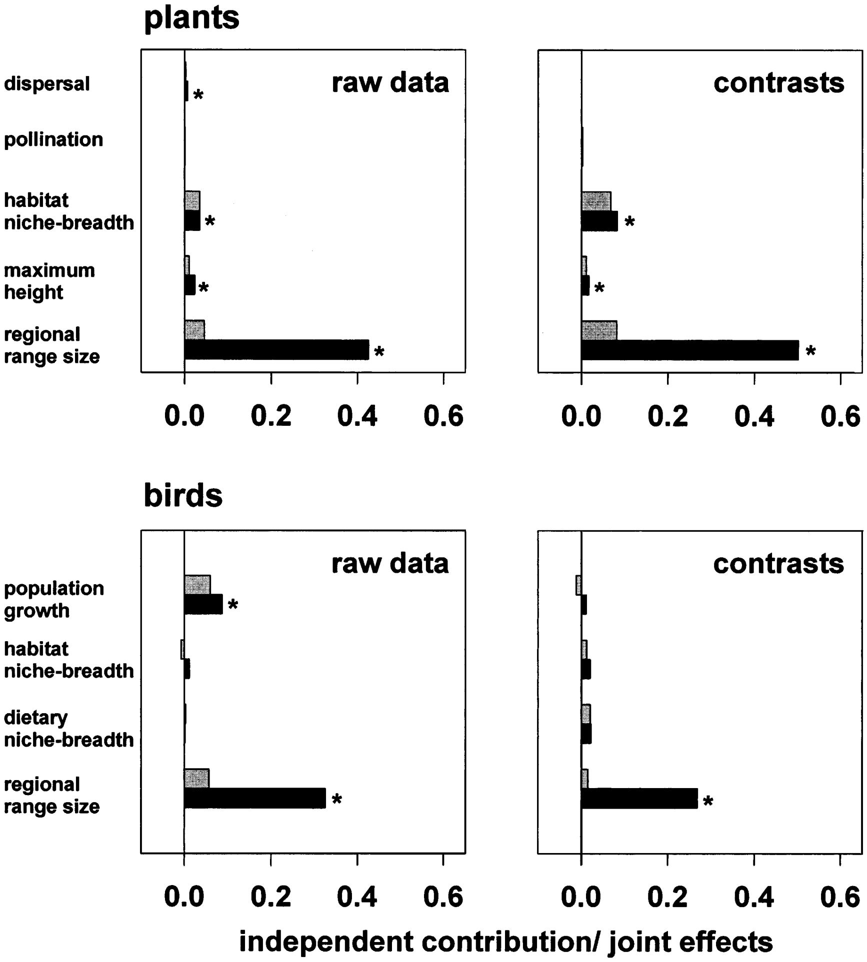
In total we recorded 95 bird species to breed across all sampled mining sites (mean = 34 ± 19 SD, range: 6–72), 61% of the regional species pool. Three out of four life history traits were significantly related to local occupancy in the analysis of raw data (Table 3): occupancy across mining sites increased with regional distribution, population growth and with habitat niche-breadth. The only non-significant variable was dietary niche-breadth. However, within the phylogenetically controlled approach population growth failed, whereas dietary niche-breadth passed significance (local occupancy increased with dietary niche-breadth). In the hierarchical partitioning the results of cross-species (Fig. 2, lower left) and the phylogenetically controlled analyses (Fig. 2, lower right) were again similar. The most important independent variable influencing local occupancy was regional range size followed by population growth. All other variables failed to explain a significant part of variance. But note that the population growth variable failed to reach significance in the phylogenetically controlled analysis.

## Discussion

For plants and birds, the most important trait which influences local occupancy of species across the non-reclaimed mining sites is regional range size. Regional range size seems to be a much better indicator of colonisation probability than life history traits or niche breadth. Thus, our attempt to understand the occurrence of species in non-reclaimed mining sites boils down to the well known correlation between local and regional distribution and an understanding of the regional patterns of distribution (e.g. Goodwin et al. 1999).

Apparently we can predict occurrence of species across non-reclaimed mining sites from studies on larger scales. Hence species common on large scales are also common on nested scales. Thus, patters of occur-

Fig. 2. Summary of the results of 4 separate hierarchical partitions. The graphs indicate the importance of independent variables for the local occupancy of plants and birds across non-reclaimed mining sites. Upper graphs: plants, lower graphs birds. The left column present the results of species data, the right column those of phylogenetically independent contrasts. Black bars correspond to independent contribution (in percentage of the variance) of independent variables, and gray bars to joint effects (for further information about hierarchical partitioning see methods). Contributions which are significant ($p < 0.05$) by a randomisation test are indicated with an asterisk.



rence across non-reclaimed mining sites are simply part of the general issue of commonness and rarity (e.g. Kunin and Gaston 1999, Gregory and Gaston 2000). Which processes operate behind the correlation between local and regional distribution? Causes and consequences of range size at different scales have been studied intensively during the last decade (e.g. Hodgson 1986, Thompson et al. 1999), nevertheless the issue is far from being settled.

Up to now it is not clear whether this correlation is due to small scale processes which add up to large scale patterns, or whether the local patterns are the result of processes which operate on larger spatial scales (see also Brändle et al. 2002b). As for many macroecological patterns, "scale-up" and "scale-down" may have some importance. A third line of thinking explains the correlation between regional and local distribution by geographic constraints, e.g. the distribution of habitats. Species which use frequent habitats are expected to be widely distributed (the "resource availability hypothesis", Hanski et al. 1993, Gregory and Gaston 2000). As long as the relative occurrence of habitats is similar on the regional scale as well as on the local scale one expects a positive correlation between regional and local distributions. Although we have no quantitative information about the occurrence of habitats within our mining sites and around, this explanation seems not very likely in the context of the analysed mining sites. As already noted habitats occurring within mining sites are special because of the low nutrient status and high acidity of soils. In the surroundings some habitats common within non-reclaimed mining sites do not occur at all (e.g. pure sands, oligotrophic waters).

Our measure of local occupancy across mining sites makes two assumptions. First, the sites are all of about the same age and second, the sites have all approximately the same size. A short look into Table 1 shows that this is not the case. Thus, not all habitats may be available in all sites and species which need large area may be absent from small sites. This bias may have influenced our results. One way to evaluate this bias is to consider presence or absence from all sites listed in

Table 1 instead of local occupancy (see also Dupré and Diekmann 1998). When we use presence absence data in a logistic regression the results are very similar to the results of local occupancy. Hence we conclude that the bias introduced by age and size differences between mining sites had only little influence on the general conclusions of our study.

The hypothesis that faster population growth increases the probability to colonise and maintain populations was only supported in the analyses of raw data but statistical significance disappeared in a phylogenetically controlled analysis. Note that we tested this idea only for birds. It is well known that parameters such as body size have a strong phylogenetic bias (Blackburn et al. 1996). The influence of population growth for colonization of mining sites may also be blurred by edge effects: obviously, non-reclaimed lignite mines are no “islands” in “seas” of unsuitable environment (Strong et al. 1984). Especially birds breeding within mining sites can also exploit dietary resources in the surrounding landscape.

Our results failed to find support for the ”pollination strategy hypothesis” for the colonization of plant species. Plant species with pollination strategies which are independent from mutualistic animals have been shown to be the first colonizers of volcanic islands (e.g. Baker and Stebbins 1965, Brown and Marshall 1981, Grubb 1987, Whittaker et al. 1989). Species which need mutualistic animals for pollination are not able to build up founder populations as long as pollinators have failed to colonize the area. Hence this pattern is also an issue of isolation. As already noted above, mining sites are no real islands and pollinators from the surroundings may do the pollination service for the plants within the mining sites.

The most simple “scale-down” process from the regional to the local scale is random sampling from the species pool. That is, colonization is much more likely for species which are abundant in the surrounding area. Salisbury (1942) and Grime (1986) coined the term “infection pressure” to describe a similar process. They hypothesized that diaspore pressure into previously unoccupied areas is largest for plants above a critical level of abundance in the surrounding area irrespective of apparent mode of seed dispersal. Note that our analyses failed to provide evidence for the importance of dispersal mode for local occupancy. This underlines the predominance of chance processes during dispersal (Cain et al. 1998, Lichter 2000). Nevertheless dispersal may be important for establishment and persistence of species at particular communities within the mining sites. Hence if we step down to smaller scales, that is to habitats within a particular mining site the picture may change. Overall, we suppose that random sampling is the most simple and straightforward explanation of local occupancy across mining sites. But note that the “niche-breadth hypothesis” and the “infection pressure” are difficult to separate as species with a broad niche may be more common and may have a large regional distribution (the “niche-breadth hypothesis” e.g. Brown 1984, Hanski et al. 1993, Gaston 1994, Thompson et al. 1999).

Plants and birds differ in their ability to locate actively suitable habitats. In both groups, however, regional range size was the most important predictor of local occupancy. Nevertheless, more bird than plant species from the respective pools were present in mining sites (61 vs 51%, $p = 0.01$). Thus, active dispersal resulted in more homogenous colonization across species in birds when compared to plants. However, an alternative explanation is that birds are in general less habitat specific than plants.

In sum, life history traits were only of minor importance to explain local occupancy and we conclude that regional patterns provide important clues to understand local community composition. However, the processes which trigger the regional patterns of distribution are not well understood. There are two avenues of ideas which need further consideration to understand the regional distributions, especially in Europe. Firstly, European ecosystems are influenced by man since > 10000 yr. Thus, patterns of regional distribution may be more the outcome of human influences than ecological processes. Secondly, Europe is at the margin of the Palearctic realm and distributional patterns may be due to the fact that many species are at the edge of their range. Nevertheless, irrespective of the background of the regional patterns of distributions these patterns are a good starting point for landscape managers to predict the flora and fauna in areas under their care.

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## Appendix 1. Plant phylogeny

Relationships among lower groups of vascular plants were taken from Doyle (1998; their Fig. 1). The relationships between families were taken from Pryer et al. 1995 (ferns), Chase et al. (1993) (gymnosperms), Dodd et al. 1999 (angiosperms), Kubitzki (1998) (monocots), Haynes et al. 1998 (Potamogetonales). For families missing in the phylogeny of Dodd et al. (1999) due to polyphyletic relationships we either used polytomies (Ericaceae s.l. = Ericaceae + Empetraceae; Globulariaceae, Plantaginaceae, Scrophulariaceae, Hippuridaceae) or phylogenies resolving the generic level (Dipsacales: Donoghue et al. 1992). Within families we used traditional taxonomy for tribes, subtribes, genera, subgenera, sections, subsections, series and aggregates (sources: Hegi 1939–1995, Tutin et al. 1964–1993. *Trifolium* was taken from Zohary and Heller (1984), Orchidaceae from Dressler (1993), Poaceae from Watson and Dallwitz (1992). Molecular based phylogenies were used for the following groups: Fabaceae (Doyle et al. 1997 [tribes], Käss and Wink 1997, Wink and Waterman 1999 [genera]), Apiaceae (Downie et al. 1998 [genera]), Asteraceae (Jansen et al. 1990 [tribes]), Poaceae (Duvall and Morton 1996, Catalan et al. 1997), Lamiaceae (Kaufmann and Wink 1994, Wink and Kaufmann 1996 [tribes]), Ranunculaceae (Ro et al. 1997 [genera])).