# Positive interactions in communities:
# a central issue in restoration

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ABSTRACT: Positive interactions within and among species are important forces in organisation of communities yet they still do not seem to be sufficiently recognised in community ecology. They are representative of self-sustaining communities and should accordingly be given a special attention in restoration, because they may significantly accelerate the assisted site recovery. To illustrate this approach, selected interactions related to dispersal and recruitment are considered. At the dispersal phase, mutualisms are the most frequent. They often include multiple species associations and various organisms. The best known are associations between foraging animals and plants which offer nutritional rewards. Commensalisms are typically recognisable in epizoochory, and un-intended dispersal by man; the importance of the latter phenomenon has substantially increased in recent years. Commensalistic interactions among plants at the dispersal phase are little known but seem to be relevant in wind-influenced ecosystems. A particularly interesting category of positive interactions represent cases in which dispersal is primarily influenced by mutualism but ultimately controlled by commensalism. In such cases, frugivores bring the collected seed into another site which they use to perch and deposite the seeds there. At the establishment phase, commensalistic interactions among plants clearly play the most important role, and the nurse effect is presently known from a wide range of ecosystems. The nurse effect may be maternally-mediated, it may involve neighbour conspecifics, or different species. The latter category most frequently includes multiple species associations. The nurse effect may in time turn into competition, but frequently it is cyclic. Of a special interest is a little known reciprocal nurse association between two species which may be regarded as a mutualism. In extreme environments, some nurse plants have substantial effect on species diversity, and possibly fulfill a keystone function. In conclusion, the author shows how the understanding of positive interactions may be used in planning and implementation of restoration schemes, and also in post-restoration monitoring.

KEY WORDS: positive interactions, mutualism, commensalism, restoration

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## INTRODUCTION

Positive interactions in communities occur in a wide range of biomes (Franco & Nobel 1989; Valiente-Banuet *et al.* 1991; Franco-Pizana *et al.* 1995, 1996; Carlsson & Callaghan 1991; Urbanska 1992, 1997; Belsky 1994; Callaway & Sabraw 1994; Callaway 1995; Shevtsova *et al.* 1995; Jones *et al.* 1997). Balance between positive and negative interac-

tions is often influenced by ecosystem productivity (Grime 1979), and may vary in time and space (Hay 1986; McAuliffe 1986; Aguiar & Sala 1994; Callaway *et al.* 1996; Wilson & Nisbet 1996; Callaway & Walker 1997).

Darwin, and also early ecologists (Clements *et al.* 1926; Allee *et al.* 1949) recognised positive and negative interactions among species, and "facilitations" have been frequently reported in studies on succession. Despite this recognition, positive interactions are typically not regarded as important community processes in contemporary texbooks and models (Kareiva & Bertness 1997). This situation has undoubtedly been influenced by the strong focus of community ecology on competition which received a considerable attention throughout a long period of time, almost to the exclusion of other interactions (e.g., MacArthur & Levins 1964, 1967; Pianka 1974; Connell & Slayter 1977; Tilman 1982). Also, it possibly resulted from the concentration of ecological research in easily accessible, and productive mesic ecosystems. Interest in some positive interactions and their evolutionary concequences increased throughout the last fifteen years (Boucher 1985; Vandermeeer 1984; Hunter & Aarsen 1988; Price 1991; Handel 1997), but only very recently the ecologists have begun to realise that a full understanding of positive interactions in communities may be helpful in resolving many long-standing conceptual problems in ecology (Lawton 1994, 1995; Bertness & Callaway 1994; Kareiva & Bertness 1997; Brooker & Callaghan 1998).

Positive interactions have complex and important implications for community diversity. The most immediate is the simple diversifying effect of species that create physical space or improve life conditions for other species. Associational defences also belong to this category. It seems, however, that positive interactions may also influence in a long run the species diversity of a community via creating new interaction webs (Hacker & Gaines 1997).

Positive interactions were generally defined as non-trophic interactions among two or more species that positively affect at least one of them (Bertness & Callaway 1994; Hacker & Gaines 1997). This definition should be modified because findings in plant population ecology demonstrate that positive interactions may also occur between conspecific partners (Walton 1922; Urbanska 1997 and unpubl.; Wied & Galen 1998; Tischew & Kirmer, personal communication).

Positive interactions in communities may include associations among conspecific individuals, multiple species associations, or an exclusive two-species partnership. They may include various species groups, or various organisms. A given species may be involved in different positive interactions depending on its life-history phase (Table 1). Last but not least, positive interactions may occur only once in life of a plant, e.g., at the pollination time. The frequency of positive interactions may vary along a gradient of stress (Hillier 1990; Callaway & Bertness 1994).

Strong abiotic stress might particularly favour the evolution of positive interactions enhancing survival. It is thus not suprising that in the situations characterised by physical stress positive interactions are often important (Franco & Nobel 1989; Valiente-Banuet & Ezcurra 1991; Bertness & Callaway 1994; Bertness & Leonard 1997; Requena *et al*. 1996, 1997; Hacker & Gaines 1997; Holmgren *et al*. 1997; Jones *et al*. 1997). However,

**Table 1.** Life-history phases and possible positive interactions in a single plant population. PD = primary dispersers; SD = secondary dispersers; M = mother plant; CP = conspecific neigbour but not the mother; DPS = different plant species; MYC = mycorrhizae; RH = Rhizobia; DSH = dark-septate hyphae associations.

| Life-history phase | Interacting partner(s) |
| --- | --- |
| Reproduction by seed | Pollinator |
| Dispersal | Disperser (PD, SD) |
| Establishment | Nurse (M, CP, DPS) |
| Vegetative growth | Symbiont (MYC, RH, DSH), neighbour plant |

physical stress does not seem to influence all positive interactions in the same way. Interactions promoting recruitment in plant populations generally increase in frequency with increasing stress, but those enhancing dispersal do not seem to follow any consistent pattern; rather, they are influenced by the specific behaviour of the partners involved.

Stress occurs not only in natural habitats. Dramatically degraded sites also qualify as stressed, because their attributes ensuring the function of communities have been lost. This loss may or may not be compounded by severe climatic factors, but is in itself sufficient to offer a particular challenge to restorationists. The important mid-term goal of restoration is the initiation of processes involved in population, community, and eco-system dynamics. Positive interactions are representative of self-sustaining communities; they should accordingly be given a special attention in restoration, because they may significantly accelerate the assisted site recovery. To illustrate this approach, I propose to consider some positive interactions related to seed[1] dispersal and establishment of plants. I will also show how the information on those interactions may be used in planning and implementation of restoration work, and also in the post-restoration monitoring.

POSITIVE INTERACTIONS AT THE DISPERSAL PHASE

Seed dispersal, also known as seed rain, includes two basically different components. One of them is a local dispersal of diaspores produced *in situ*, the other one – the dispersal beyond the production site. The dispersed diaspores may be deposited *(i)* in their original population, *(ii)* in another, already existing, population, *(iii)* in a site where a population existed before but became extinct for various reasons, or *(iv)* in formerly uninhabited sites. Considered on a site level, seed rain may consist exclusively of locally produced seeds, it may include only the seeds which immigrated from more or less distant sources, or it may include both components.While occurrence of vegetation in a site does not

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[1] The term "seeds" is used in a generalised way to design various diaspore types (genuine seeds, achenes, kernels, etc.)

necessarily mean that all diaspores in the seed rain are produced by the extant plants, seed rain in a site with bare soil obviously implies diaspore input from outside.

The fates of diaspores depend both on primary dispersal, and on a secondary dispersal from the place of the first deposition (Janzen 1983; Van der Wall 1992; Chambers 1995 a–b; Chambers & MacMahon 1994; Handel 1997; Hoshizaki *et al*. 1999).

Mutualistic associations at the dispersal phase occur between forage plants and their dispersers which are offered nutritional rewards (dry or arillate seeds, elaiosomes, fleshy or non-fleshy fruits). A given zoochorous species may have various dispersers. For instance, *Trillium ovatum* in mesic forests of the Rocky Mts is principally myrmecochorous (Handel & Beattie 1990), but its fruits may also be dispersed by yellow jackets (Jules 1996, Jules & Rathcke 1999). The fleshy-fruited saguaro cactus *Carnegiea gigantea* from the Sonoran Desert is dispersed by almost all desert dwellers including man (Olin 1977; Urbanska, personal observations). Fleshy-fruited trees in a Philippine submontane rainforest are visited by a wide spectrum of frugivores, but the relative numbers of dispersers vary in relation to seral stages: early-successional species have more dispersers than the mid-successional, and the late-successional, most specialised species (Hamann & Curio 1997).

Typical mutualisms involved in endozoochory have different spatial aspects. In some cases, the seed deposition takes place either directly beneath the seed source or within an exceedingly limited radius. This pattern was observed e.g., in bird-mediated dispersal of fleshy-fruited woody plants at forest edges (Kollmann, personal commmunication, see also Kollmann & Pirl 1995; Kollman & Schneider 1999). In other cases, the dispersers take the seeds away from the source and bury them in caches. Some of those associations are truly spectacular, as exemplified by the behaviour of the nutcracker (*Nucifraga caryocacactes* L.), the principal disperser of Arolla pine (*Pinus cembra* L.) in the Alps. The bird may fill up its crop with up to 134 nuts for one transport, so that sometimes it has problems with the "take-off". The subsequent seed burials include 2–11 nuts per cache. The forgotten caches of the nutcracker represent the most effective factor in regeneration of *P. cembra* in the Alps (Campell 1950).

Positive interactions involved in dispersal by animals are not limited to endozoochory. Less frequent but equally interesting are the mutualisms between plants and birds which use woolly or plumed diaspores as the nest-building material. The case of the snow finch *Montifringilla nivalis* L. is particularly instructive: this typical inhabitant of the alpine and the subnival belt of the whole Swiss Alps was reported to nest up to 3476 m a.s.l. (Géroudet 1957). I recently observed on an extreme high-alpine site (ca. 2700 m a.s.l.) numerous woolly diaspores of *Salix herbacea* braided into the nest of *M. nivalis*.

Not only mutualisms but also commensalisms are recognisable at the dispersal phase. The best understood are epizoochory and an un-intended dispersal by man. Passive transport of seeds by attachment to wool or fur may cover very long distances, but it is strongly influenced by the behaviour of the animal (Milton *et al*. 1990; Fischer *et al*. 1996; Stanton & Galen 1997). Direct attachment of diaspores on clothes and footwear (Clifford 1956) is becoming increasingly important as dispersal factor, because human behaviour during recreation time has changed significantly in the last years. Vehicles, or

**Table 2.** Seed input (total number and % of total) in open pastures and secondary vegetation islands in Poco das Antas Biological Reserve, Brasil. Data for all trap pooled over the 11-month sampling period. VD = vertebrate-dispersed woody species; FS = forbs with unspecified short-range dispersal; OS = wind-dispersed species, vines, and unknown forms. Modified after Kolb (1993).

| Sample area | Seeds total | VD | FS | OS |
|---|---|---|---|---|
| Open pasture | 13 702 | 0.05 % | 80.1 % | 19.9 % |
| Islands of vegetation | 37 190 | 8.90 % | 19.7 % | 71.4 % |

agricultural machinery may also be very effective dispersal agents (Krach & Koepff 1980; Mortimer *et al*. 1993; Strykstra *et al.* 1996).

Commensalism at the dispersal phase may be also recognised in associations in which plants only are included. Such associations were not much studied in detail, but recent reports suggest that they may be important under certain environmental conditions. The documented cases show relationships between a successful seed input and the occurrence of plants at the deposition site, esp. in areas influenced by high winds. For instance, Kolb (1993) found that seed input in islands of secondary vegetation occurring in degraded pastures of Brasil was about three-fold larger than in adjacent open pastures (Table 2). Positive effect of the extant vegetation on seed deposition was documented also in a recent study on the high-alpine species *Phyteuma hemispheaericum*. According to Muller-Schneider (1986), *P. hemisphaericum* is wind-dispersed; however, its seeds are deposited exclusively in the immediate vicinity of the mother plants which apparently protect seeds from mechanical stress caused by high winds (Maier *et al*. 1999). Similar dispersal patterns were observed in other high-alpine plants, e.g. *Trifolium thalii* (Hasler 1992; Urbanska unpubl.) and *Lotus alpinus* (Urbanska 1994). The available data from various parts of the world show that dispersal distances in the alpine vegetation belt are for the most part exceedingly short (Marchand & Roach 1980; Spence 1990; Stocklin & Bäumler 1996; Pflugshaupt 1997; Urbanska 1997; Urbanska *et al.* 1998; Urbanska & Fattorini 2000; Urbanska *et al*. 1999). Future studies may provide a further evidence of seed deposition within mother plant canopy or in its immediate vicinity.

The dispersal distance seems to be positively influenced by the height of the mother plant (Sheldon & Burrows 1973). High-alpine plants are for the most part low-growing and this feature clearly represents a part of a survival-promoting strategy. It is conceivable that the exceedingly short dispersal distances and the positive interactions occurring among plants at the dispersal stage might represent further components of this strategy in the highly-stressed alpine environments. Further studies are required to clarify this intriguing problem, and quantitative comparisons would be particularly desirable.

Some positive interactions observable at the dispersal phase may be rather complex and involve at least three different species, with a different function each. This category includes cases in which frugivorous dispersers which fed before on fleshy-fruited plants are attracted on another site by plants which offer them not nutritive rewards but perching and roosting places. The subsequent deposition of seeds is thus enhanced by plants
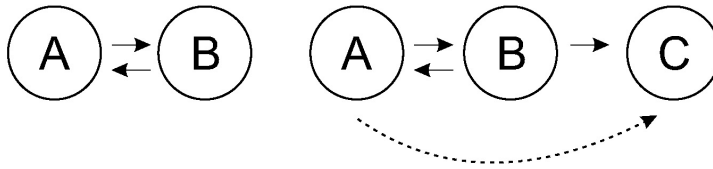
**Fig. 1.** Typical mutualism (left) and mutualism + commensalism (right) at the dispersal phase. Capitals "A", "B" and "C" refer to different species involved.

not involved in the actual foraging. Many such cases were regarded by previous authors as mutualisms (see e.g., Handel 1997) but in fact they represent mutualism combined with commensalism (Fig. 1). Dynamic development of vegetation resulting from such interactions was well documented in some recent studies. For instance, isolated residual trees proved to be more important as perches than food source to frugivores which brought seeds of numerous indigenous species into a heavily degraded, former subtropical forest site (Toh *et al*. 1999). Experimental studies demonstrated that planting of container-grown shrubs and trees on an open site attracted the birds carrying seeds of various species, and that the height of plants providing perches was important (McClanahan & Wolfe 1993; Robinson *et al*. 1992; Robinson & Handel 1993; Handel 1997). Woody species planted in clusters functioned particularly well (Table 3).

**Table 3.** Deposition of seeds beneath clusters of woody species planted in an open field. Modified after Handel (1997).

| Number of plants per cluster | Seeds per cluster |
|---|---|
| 7 | 3203 |
| 21 | 1996 |
| 42 | 4921 |
| 70 | 4137 |

POSITIVE INTERACTIONS AND RECRUITMENT

Even the most successful seed rain or the best-developed seed bank does not suffice if the plant establishment is not possible (Fig. 2)**.** Safe sites promoting survival and recruitment represent thus the crucial element in plant population dynamics. Safe sites are ecosystem-specific; they should be characterized by hierarchy of environmental risks from which they should protect newcomers (Urbanska 1995, 1997; Urbanska & Schütz 1986). Safe sites are required not only for recruitment from seeds and/or specialized vegetative propagules (e.g., those of *Polygonum viviparum*), but also to a successful establishment of ramets in the "guerrilla" plants with the loose clonal growth (e.g., *Geum reptans*, or *Trisetum distichophyllum*, Urbanska 1992 and unpubl.).

Neighbour plants often function as safe site components. These commensalisms were
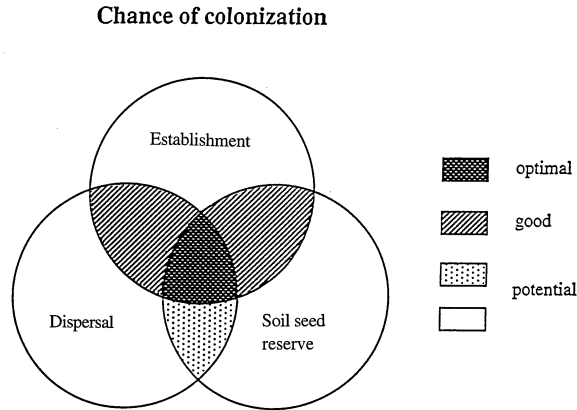
Chance of colonization



**Fig. 2.** Relationships between dispersal, soil seed reserve, and establishment. Modified from Urbanska and Chambers (in press).


termed "nurse effect" (Shreve 1910) and originally described from the Sonoran Desert (Shreve 1931), but since observed not only in more semi-arid sites of this area (e.g., Turner *et al.* 1966; Nobel *et al.* 1986; Franco & Nobel 1989), but also in a wide range of other stressed environments, e.g., subarctic and arctic tundra (Carlsson & Callaghan 1991; Bliss & Peterson 1992), forest-alpine tundra ecotone (Holtmaier & Broll 1992); high-alpine sites (Urbanska 1992, 1997b and unpubl.; Wied & Galen 1998; Gigon 1999), or alpine-subnival ecotone (Kividze & Nakhutsrishivili 1998). They were also reported from a dry limestone grassland in lowland (Ryser 1993; Cerletti 1997).

The nurse effect may involve conspecific (Fig. 3) or heterospecific interactions. The conspecific nurse effect may be maternally-mediated, i.e. represent a form of parental care (Walton 1922; Urbanska 1997b; Wied & Galen 1998; Tischew & Kirmer, personal
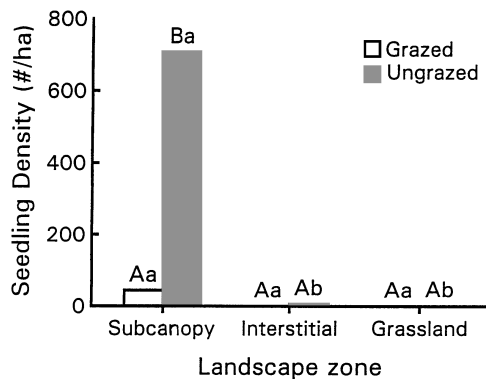


**Fig. 3.** *Quercus emoryi*: density of < 1-y-old seedlings in three subcanopy, interstitial, and grassland landscape zones on grazed and ungrazed sites in SE Arizona, USA, in 1993. Different uppercase letters indicate statitically significant (*P* < 0.05) differences between means within landscape zones. Different lowercase letters indicate significant (*P* < 0.05) differences between means within grazing history. Figure provided by courtesy of Dr. J. F. Weltzin.

communication); the nurse function may also be provided either by adult conspecifics, or e.g., aggregated juveniles of the same cohort (Urbanska 1992, and unpubl.). The heterospecific nurse associations are most varied and include different plant groups or different life forms (Urbanska 1997b). Most frequently they represent multiple species associations of two kinds: *(1)* one species may have several nurses, or *(2)* one nurse may serve several protégés. While the associations between the protégé and each of its nurses are clearly separated by some distance, the nurse effect in a single plant sheltering several protégés occurs within a limited space occupied by the nurse canopy. For instance, establishment of the saguaro cactus *Carnegiea gigantea* in the Sonoran Desert is promoted by *Cercidium microphyllum* (Fabaceae), *Fouguieria splendens* (Euphorbiaceae), *Larrea tridentata* (Zygophyllaceae) or *Ambrosia deltoidea* (Asteraceae); the relative frequency of particular nurse associations may significantly differ in function of the habitat and the aspect (Parker 1988, 1989). On the other hand, a single cushion of moss campion *Silene acaulis* in the Alps does not usually exceed ca 30 cm in diameter, but may nurse at the same time *Cirsium spinosissimum*, *Erigeron uniflorus* (Asteraceae), *Trisetum spicatum* (Poaceae) and *Phyteuma hemisphaericum* (Campanulaceae); comparable patterns were registered also in subarctic tundra (Urbanska unpubl.)

The nurse effect clearly improves some site factors but also affects the others. Accordingly, it will outweight the costs of negative change only when a given environmental hazard the nurse protects from, poses a principal constraint to plant recruitment (Holmgren *et al*. 1997). For instance, the shelter from frost and wind in high-alpine environments (Urbanska & Schütz 1986; Urbanska 1997b), or that from desiccation and herbivores in semi-arid areas (Franco & Nobel 1989; McAuliffe 1986) is apparently more important that the light level reduction under the nurse canopy. It may also be that complementary rather than competing root systems between nurse and protégé help to balance the positive and negative factors (Cody 1993).

The commensalistic associations between nurses and the nursed plants may be replaced in time by competition (McAuliffe 1984), but they also may undergo cyclic changes (Vandermeer 1980; Cody 1993). For instance, the creosote shrub *Larrea divaricata* in the Chihuahuan Desert nurses *Opuntia leptocaulis*, becomes temporarily outcompeted by the latter species, but re-establishes in the open spaces vacated by the dead or dying individuals of the cactus (Yeaton 1978). A comparable sequence in space occupation was observed in the *Acacia schaffneri-Opuntia streptacantha* vegetation in central Mexico (Yeaton & Romero Manzanares 1986). An exceedingly interesting facet of the temporal changes in the nurse-protégé associations is that in some circumstances pairs of the involved species may serve reciprocally as nurses to each other. In such cases, commensalism turns into a symbiotic association. For instance, *Ambrosia deltoidea* nurses seedlings and juveniles of *Carnegiea gigantea* but also occurs in higher densities under adult saguaros (Hutto *et al.* 1986). This reciprocal nursing might be helpful in explaining co-dominance of the two species in certain arid vegetation types of the Sonora Desert. Reciprocal nursing was also reported for *Opuntia acanthocarpa* and *Thamnosma montana* in the Mojave Desert by Cody (1993) who also proposed a loop analysis for long-term dynamics of reciprocal nursing (Fig. 4).
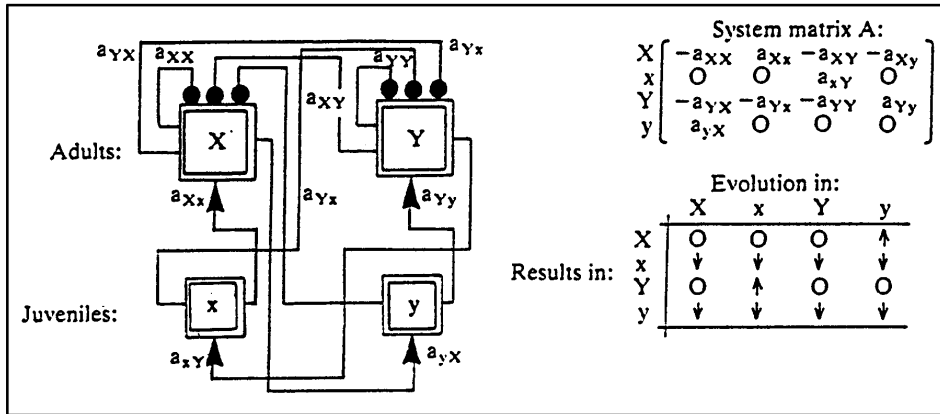
**Fig. 4.** Loop diagram of two plant species, X and Y, with a reciprocal nursing association: adults **X**, **Y** act as nurse plants for juveniles **y**, **x**, of the other species. Negative interactions are shown with circular termini, positive ones with arrows. Adults compete, and are self-damped; juveniles compete with nurses but are favoured by their nurses and then contribute to the adult populations. The system matrix is shown at the upper right, whereas the effects of evolution within each of the four components are shown at the lower right. Note that evolution within the protégé does not favour the protégé directly, but indirectly via boosting the density of the respective nurse plants. No other evolution in this system favours the component in which it actually occurs, but instead produces either no change or a reduction in the population density of the various system components. Reproduced by permission from Cody (1993), where the full theoretical analysis is provided.

In extreme ecosystems, nurse efect plays an important role on different spatial levels. On the landscape scale, it may be a determinant of vegetation pattern. At more local scales, it controls patterns of recruitment and distribution of species within terrestrial plant communitiers (Callaway *et al*. 1996; Weltzin & McPherson 1999).

Nurse plants in stressed environments have substantial effect on species diversity (Callaghan & Emanuelsson 1985; Alexandrova 1988; Suzan *et al.* 1996). They may also be particularly beneficial to rare or sensitive species (Nabhan & Suzan 1994). It may be assumed that some nurse species fulfill a keystone function in some communities.The nurse effect offers an exciting research subject, and should be further studied in different environments.

## POSITITVE INTERACTIONS AND RESTORATION

The information gathered in basic research on positive interactions may well be used in planning and implementation of restoration schemes. It has therefore to be considered in the damage assessment, and in the decisions concerning the restoration procedures. It also is helpful in post- restoration monitoring.

Consider a bare or virtually bare site located within a landscape which includes remnants of natural vegetation. As far as the degraded site itself is concerned, data on the topsoil permit to estimate not only a potential for self-recovery of vegetation via recruit-

ment from seed banks, but also possible symbionts. Data on seed rain represent a further useful information on site conditions. For instance, a machine-grade alpine ski run received only 96 seeds per m$^2$ whereas the seed rain in the adjacent natural grassland was significantly higher and also included much more species (Urbanska *et al.* 1998). Last but not least, native species which may occur scattered in a degraded site should be carefully examined.

Information regarding distances separating the degraded site from remnants of natural vegetation in the area is a first step towards the restoration planning. The second step represents inventory of communities occurring in natural sites, and of the respective dispersal modi of plants forming part of these communities. If dispersal and seed deposition are influenced by positive interactions, appropriate site manipulations may significantly accelerate the seed input. For instance, perches provided in a closed landfill for birds feeding on native woody plants in the surroundings spectacularly accelerated the addition of new species to the restoration site (Robinson *et al.* 1992; Robinson & Handel 1993; Handel 1997). Another feature which may be relevant to choice of plants for restoration in some sites is a possible negative relationship between the seral stage of a given species and the number of its dispersers (Hamann & Curio 1999).

The occurrence of vegetation apparently enhances seed input, and this interaction is very useful to restoration. A local use of transplant groups represents thus an unquestionable strategy in contemporary restoration schemes, not only to enhance survival and possible seed production in situ, but also to improve seed deposition.Transplants of species representing various life forms may be grown from seed (e.g., Robinson & Handel 1993), from clonal ramets (e.g., Urbanska *et al.* 1978), or used in form of brush bars (Densmore & Karle 1999). A further important benefit of the transplants use is that they often function as nurses to their own offspring or to the immigrating species (Urbanska 1997b–c). The selection of species included in the restoration material should be clearly based on data on natural vegetation, and a preliminary survey of physical neighbourhoods might be helpful in detecting some potential nurses.

Post-restoration monitoring should be mandatory since it is essential if ecological predictions are to be improved (Bradshaw 1996). Positive interactions related to dispersal and recruitment may be monitored indirectly and also directly. For instance, dispersal by birds may on the one hand include inventories of species visiting the restoration site and the frequency of the visits, and on the other hand direct assessment of seed deposition via study of traps. The nurse effect may be monitored with more general demographic methods (e.g., census of all juveniles in a given stand), or studies on particular species associations.

CONCLUSIONS

Positive interactions require further basic ecological research. There is an urgent need for both more case studies as well as the conceptual approaches with focus on evolutionary aspect. Further models which include both positive and negative interactions, as e.g. that recently proposed by Brooker and Callaghan (1998), would be most desirable.

The focus of restoration ecology is on process, function, and interactions (Bradshaw 1983). Positive interactions may be common, predictable, and pervasive forces in natural communities, and particularly in extreme environments. Their better understanding is accordingly vital to restoration. Such an outlook may be helpful in maintaining biodiversity (Willson 1996), esp. in managed landscapes.

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