Resilience of Mediterranean and desert vegetation after disturbance

CLAUS HOLZAPFEL1, HADAS A. PARAG1 and AVISHAI SHMIDA2
1Department of Biological Sciences, Rutgers, the State University of New Jersey, Newark, 195 University Ave., Newark NJ 07102-1811, United States of America
2Department of Evolution, Systematics and Ecology, Hebrew University of Jerusalem, Givat Ram, Jerusalem, 91904, Israel

The time and course of succession after disturbance is expected to differ in relation to environmental stress prevalent in ecosystems. In this respect arid regions are predicted to display very slow recovery after initial perturbation thus showing relative small resilience in comparison to less arid ecosystems. To test these assumptions we studied the vegetation development after experimental small-scale disturbance using an almost 20 year data set in two adjacent, yet climatically contrasting sites along a sharp gradient in Israel and the West Bank. Multivariate analysis revealed that the desert site is characterized by strong rainfall driven inter-annual variation of community composition and structure that is shared by disturbed and undisturbed sites alike. Most disturbed sites behave like undisturbed sites and therefore appear to be very resilient to disturbance. In the semi-arid and therefore comparatively less stressful Mediterranean site, in contrast, the development on perturbed plots is distinctly different from undisturbed sites and suggests a longer successional development and/or comparatively less resilience to disturbance. This apparent contradiction to the stated prediction might be related to differences in species characteristics as annual plants predominate in the desert sites and long-lived shrubs play a larger part in the vegetation of the Mediterranean site. This illustrates the importance of considering the particular life-strategies of organisms within communities when predicting the resilience of ecosystems.

Key words: aridity, succession, perturbation, plant communities

Introduction

The question whether biological communities once perturbed, i.e., moved away from their original states by disturbance, will change back to the original state is central to community ecology (McIntosh 1980). Directed community change with predictable endpoints that are defined largely by abiotic, large-scale factors (e.g., climate, soils, hydrology, etc.), the traditional Clementian model of succession (Warming 1896, Cowles 1899, Clements 1916), has long been assumed to be the norm in community development (McIntosh 1999). However, as in any ecological field of inquiry, increasingly alternative processes have been hypothesized (Gleln-Lewin and van der Marel 1992, Walker and del Moral 2003) – namely the possibility of multiple successional end-points or alternative ecological states that are defined as biotic assemblages and environmental conditions that persist at a particular spatial extent and temporal scale (Sutherland 1974, Sutherland 1990, Petraitis and Dudgeon 1999, Suding et al. 2004). These predictions are increasingly being used to model community development as the result of unprecedented large-scale climatic changes or other human induced environmental change (Schefter et al. 2001) or to define assemblage structure in severely degraded and therefore unpredictable sites (Nyström et al. 2000). Such models of alternate states include feedback mechanisms that reinforce their persistence in space and time (Van de Kopp et al. 2001). The question of whether successional endpoints are being predictable by overall climate and edaphic factors or whether they are more dependent on rather small-scale, often human-induced, impacts (Houseman et al. 2008), stands at the core of the concept of community resilience. Simply put, a highly resilient community will approach in a reasonable time frame its original state, a less resilient community will not. Such a measurement of resilience needs to be conducted on comparison of different communities.

Directional, successional vegetation changes after disturbance have been documented for a wide range of climatic zones and many successional series in temperate regions indeed approach in their community structure and composition stable end stages that resemble the conditions prior to disturbance (Schmidt 1988, Pickett et al. 2001, Bornkamm 2006). Successional dynamics in arid ecosystems are much less understood than in more mesic ecosystems. Rates of secondary succession are often considered to be relatively slow and it also has been assumed that deserts lack or have fewer successional stages (series). Despite a long history of research on succession in arid and semi-arid region, such a consensus does not appear to exist for water-limited ecosystems. Early investigators assumed that desert vegetation changes extremely slowly and will therefore show little sign of succession or regeneration after perturbation (Shreve and Hinckley 1937, Shreve 1942). Such slow speed of community change was confirmed by later studies, most of them on disturbed lands in deserts and semi-arid grasslands (Wells 1961, Webb and Wilshire 1980, Webb et al. 1983, Knapp 1991, Bolling and Walker 2000).

This perceived slow change suggests the need of sufficiently long-term studies in arid environments. These are relatively rare, with a notable exception of the Tumamoc Hill study (Arizona, Sonoran desert) that has been established in 1905 and documents the regeneration of Sonoran Desert scrub vegetation after grazing ceasement (Shreve and Hinckley 1937, Goldberg and Turner 1986, Guo 2004). Studies that infer successional change from using time-series of abandonment, so called space for time substitution (Pickett 1989), are for obvious practical reasons more common (e.g., Coffin et al. 1996, Bolling and Walker 2000).

Vegetation on less arid regions adjacent to deserts, as for instance semi-arid Mediterranean vegetation types, are expected to show faster regeneration after disturbance and more complete successional series
are expected to occur in particular post fire (May 1990, Callaway and Davis 1993) or after agricultural abandonment (Casado et al. 1988, Bonet 2004). It can be hypothesized that the long history of intense human-impact especially in the Mediterranean Basin, is one of the leading factors of the formation of resilient vegetation types (Grove and Rackham 2001). These plant communities are adapted to frequent human disturbance by being able to regenerate quickly after impact.

Bolling and Walker (2000) point out that most studies of succession in deserts do not emphasize enough the argument that successional trajectories are highly dependent on soil conditions. As different human-caused disturbance will affect soil properties differently, developing vegetation will be altered by the type and intensity of disturbance. This has been clearly demonstrated in experimental studies conducted in the Negev Desert of Israel that showed that contrasting types of soil disturbance were colonized by very distinct plant communities (Boeken and Shachak 1994, Boeken and Shachak 1998).

In order to address the question whether vegetation types of semi-arid or arid regions are less resilient to disturbance, we present here a case study in which we followed the vegetation dynamics of experimentally disturbed plots for almost 20 years after impact. For this, we compared a range of different small-scale soil disturbances that were intended to mimic the major types of human impact present in the area. Since direct comparison of resilience among areas with contrasting climates are rare, we compare in this analysis the vegetation dynamics of two adjacent, yet climatically very distinct sites, a semi-arid Mediterranean open shrubland and an arid, rocky desert site.

At the onset of the study in 1988 we initially hypothesized that the Mediterranean site will show larger resilience than the desert site. In the climatically less stressful Mediterranean site we expected to witness a faster regeneration of the vegetation.

Material and Methods

Site description

The two sites that are compared in this study are the endpoints of an aridity gradient in Central Israel and the West Bank ranging from semi-arid Mediterranean climate to extremely arid desert that has been the theatre of a range of ecological investigations by us (e.g., Holzapfel and Schmidt 1990, Holzapfel et al. 1992, Holzapfel et al. 1993, Holzapfel et al. 1995) and other groups of investigators (e.g., Kutil et al. 1995, Kutil et al. 1998, Perriente 2000). Although the two selected sites, Har Ya‘alah in the Judean Mountains (the Mediterranean site) and Khirbet Mezin in the Judean Desert at the shores of the Dead Sea (the Desert site), are only roughly 40 km apart from each other, they differ markedly in their abiotic and biotic environment (see Table 1). The climate contrasts between the two sites markedly due to a combination of the pronounced rainshadow effect on the lee side of the Judean Mountains and due to the stark elevational contrast of 1020 m gradient.

Mainly due to these climatic differences (and to a lesser extent due to edaphic and land-use differences) the vegetation types contrast between the two sites markedly. The Mediterranean site is covered by open Mediterranean-type shrubland with large shrubby oaks (Quercus calliprinos, nomenclature after Danin 1998) and dominated by the shrubs Sarcopoterium spinosum and Cistus spp. with a diversity of herbaceous plants (mostly annual but also perennials) filling the gaps between shrubs. The desert site is situated on an open rocky desert bajada and supports very sparse shrubs cover (e.g., Anabasis setifera, Zygophyllum dumosum) and a matrix of annual species and a few geophytes. More detailed descriptions and aspect photos of the vegetation can be found in Holzapfel et al. (1993) and a photo documentation of the strong effects of inter-annual rainfall variability in the desert site is in Holzapfel (2008). The two sites differ strongly in species richness and primary production (Table 1).

<table>
<thead>
<tr>
<th>Position</th>
<th>Mediterranean site</th>
<th>Desert site</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m, above sea level)</td>
<td>31°45'05&quot; N, 35°02'23&quot; E</td>
<td>31°40'54&quot; N, 35°26'28&quot; E</td>
</tr>
<tr>
<td>Average temperature (°C)</td>
<td>620 to 660</td>
<td>25</td>
</tr>
<tr>
<td>Mean annual precipitation (mm)</td>
<td>18</td>
<td>90</td>
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Precipitation (mm) in

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<tr>
<td>3 year mean</td>
<td>554</td>
<td>543</td>
<td>400</td>
<td>426</td>
<td>525</td>
<td>653</td>
<td>609</td>
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Soil type

<table>
<thead>
<tr>
<th>Mediterranean site</th>
<th>Desert site</th>
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<tbody>
<tr>
<td>terra rossa, brown rendzina</td>
<td>regosol, lithosol</td>
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Plant species richness

| km² | 418 |
| m² | 244 |
| m² (mean for years 1-4 in control) | 25.9 |

Above-ground plant biomass in control sites (g m⁻² dry weight, mean ± 1 SE)

<table>
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<tr>
<th>Mediterranean site</th>
<th>Desert site</th>
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<tr>
<td>782.7 ±13.2</td>
<td>16.6 ± 4.5</td>
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Life form (% of annuals in control plots, mean based on abundance)

<table>
<thead>
<tr>
<th>Mediterranean site</th>
<th>Desert site</th>
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<tbody>
<tr>
<td>33.9</td>
<td>92.5</td>
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* years denote growth season (Nov-May)
Experimental treatments

The sites were set up in the fall of 1988 before the first rainfalls of the season. Small test plots of 1x1 m size were selected in five randomly chosen blocks of six single treatments and one control each and marked permanently. Within each block we assigned the plots to either be control (no further treatment) or one of the following 6 soil treatments: (1) Depression – creation of a shallow 15 cm deep depression; (2) Input – turberation of surface soil and replacement of 50% original soil volume by coarse gravel and washed dune sand; (3) Fertilization – turberation of surface soil (0-15 cm) with input of commercial 220 g/m² NPK fertilizer; (4) Sealing – covering of soil surface with roofing paper to create run-off, the sampling area consisted of edges with a comparable total area of 1 m²; (5) Turberation – turberation of surface soil; (6) Removal – removal of above-ground vegetation and litter without change of soil surface structure.

These experimental disturbances were designed to mimic human-caused disturbances that were found in the surroundings and were compared to them in related studies (for details see Holzapfel 1994).

As these experimental disturbances treatments each combined various separate impacts (e.g., vegetation removal, changes in soil structure that were expected to increase water availability, changes in nutrient availability), we used for the analysis a single disturbance index, a numeric value, which we assigned to each of the six treatments. These values are designed to reflect the disturbance intensity by factorizing the separate impacts. Thus we could quantify the experimental treatments along an estimated gradient of disturbance intensity and we ranked the treatments in the following manner (from highest intensity to lowest): Depression = 4.5, Input = 3.5, Fertilization = 3, Sealing = 2.5, Turberation = 2, Removal = 1, Control = 0. We used these values as predictors of community structure in one of the multivariate analysis (see below). To our knowledge the sites were not disturbed since the implementation of our treatments.

Vegetation sampling and multivariate data analysis

In the years following disturbance we sampled the vegetation during the peak of the vegetation by determining identity and estimating aerial cover of all species within the plots. The plots were sampled in the four years after disturbance, in the 6th year and the 14th and 19th years (see Table 1).

For analysis we averaged species cover data for each treatment among the five blocks in order to reduce variation of data that arose due to small plot size (detailed information about species composition and variation among plots are found in Holzapfel 1994).

Data were analyzed separately per site in Detrended Correspondence Analysis (DCA) using CANOCO version 4.5 (Ter Braak and Smilauer 2002). As this method allows placement of calculated species and site scores (as weighted averages) in multidimensional space, we were able (a) to relate treatment trajectories to representative species that characterize these treatments and (b) to compare the community composition and structure between plots. For the former we focused on three comparisons of plot location in DCA space: 1. Euclidian distance of treatments to control thereby assessing the relative effect of treatments, 2. distance between treatments thereby assessing the effect of different treatments, and 3. distance to the first year thereby quantifying the extent of change.

To further investigate the effects of selected key parameters we entered the predictors rainfall, disturbance intensity, and age of plot (year since disturbance) into a Canonical Correspondence Analysis (CCA) that otherwise used the same plot data as the DCA. In the presented graphs for both analyses we show for both analyses only species with an importance weight above 10% (Desert site) and 20% (Mediterranean site), even though all species were used in the analysis (59 total in the Desert site and 244 species in the Mediterranean site).

![Diagram](https://via.placeholder.com/150)

**Figure 1.** Ordination diagram based on Detrended Correspondence Analysis (DCA) of plant communities on treated plots and non-treated controls. Each separate panel shows the temporal development of site scores as trajectories of a single treatment (full circles) in comparison to control (open circles). Treatment abbreviations: C = control, D = depression, F = fertilization, I = input, R = removal, S = sealing, T = Turberation. The scores of characteristic species are given as well (crosses with adjacent letters). (a) Mediterranean site (eigenvalues for DCA axes 1 and 2 are 0.181 (Monte-Carlo = 0.016) and 0.105, respectively. Species abbreviations: AB = Avens barbata, AS = Avens stenula, BD = Brachypodium distichum, CC = Citrus cretica, CS = Citrus salviifolius, HS = Helichrysum sanguineum, LC = Lagascea cumuloides, LR = Lolium rigidum, RT = Rubia teresfolia, SS = Sarcopoterium spinosum, TP = Trifolium purpureum, TT = Trifolium tetragonum. (b) Desert site (eigenvalues for DCA axes 1 and 2 are 0.298 (Monte-Carlo = 0.030) and 0.177, respectively. Species abbreviations: AF = Aarrosiaea factoroskis, AP = Asteriscus pygmeus, FR = Eucalyptus rostrata, IT = Limonium thonii, MA = Matthiola aspera, MI = Medicago lacinata, NB = Notoceras bicorne, PD = Pteranthus dichotomus, PO = Plantea pavata, SC = Stipa capensis, TS = Trigonella stellata.)
Results

Vegetation development after disturbance
In the Mediterranean site control plots changed in community structure over time only moderately. The DCA-trajectory for control plots (Figure 1a) indicates only a slight shift in characteristic species. In comparison to this, the community structure of some treatments shifted considerably. Such strong temporal change is indicated by comparatively long trajectories for the fertilization and input treatments. Intermediate trajectories were found for the removal, turba- tion, and depression treatments while only little community change was visible the sealing treatment. Communities on control sites were characterized by a mix of perennial species: Sarcopoterium spinosum, Cistus creticus (both shrubs), Rubia tinifolia (chamaephyte), Helichrysum omeoense (hemicycrophyte), and the only characteristic annual plant was Lagocera cuminoides. In clear contrast to this, the disturbed sites were initially characterized by a set of annual species (Trifolium pupleinum, Brachypodium distachyon, Lolium rigidum, Avena sterilis) and further developed towards communities characterized by the annuals Avena barbata and Trifolium tenuifolium and the shrub species Cistus salvifolius.

Undisturbed plant communities in the Desert site (control, Figure 1b) did change considerably from year to year and over the full span of the 19 years seem to describe an almost circular trajectory with different species characteristic for different years. The communities of almost all disturbed plots changed either less (fertilization and input treatments) or to a similar extent (removal, turba- tion and sealing treatment) to control plots and were characterized by the same set of species as the control. The only exception is the depression treatment, in which communities distinctly moved away from undisturbed sites. Here the species Limonium thyminii and Sisca cap- ensis were characteristic.

Difference of treatments to control
The plant communities that established in the disturbance treatments in the Mediterranean site showed, after initial change in year one, in the following three years a trend of becoming more similar to the control (Figure 2a). In the following years this trend however reversed and after 14 and 19 years most treatments actually became more different from the control. This was most prominent for the removal, fertilization and input treatments. The exceptions to this seem to be the communities that developed after the creation of a depression which was very similar to controls after 14 years and became more different again 4 years later. The development in the desert site was very different from the Mediterranean site (Figure 2b). Treatment sites varied very much from year to year in their difference from control in the initial four years but seem to become more similar to controls in the later years. The one exception is the depression treatment which was characterized by large differences from the control even in the later years.

Heterogeneity among treatments
The plant communities in different treatments in the Mediterranean site became increasingly different from each other over time, while in the desert site no such clear temporal trend is seen (Figure 3). In the desert only initial fluctuation from year to year is evident, variation among treatments in later years is comparatively low and constant.

Community development from initial year
Overall, the Mediterranean site is characterized by a steady increase in community differentiation that signifies clear community change (Figure 4a). For almost all treatments the largest differences are

![Graph showing temporal development of heterogeneity among treatments.](image)

**Figure 3.** Temporal development of heterogeneity among treatments. Shown are the means ± SE of all possible Euclidian DCA distances between treatments calculated within a given year. Full circles represent the Mediterranean site and open circles the Desert site.

![Graph showing temporal development of community differences between treatment and control.](image)

**Figure 2.** Temporal development of community differences between treatment and control. The presented Euclidian distances are related to the relative effect of treatments. (a) Mediterranean site, (b) Desert site. Treatment abbreviations see legend to Figure 1.
found after 19 years. It therefore appears that the communities became increasingly different from the initial stage. In sharp contrast, the desert site (Figure 4b) did not show such an increase over time. An initial increase in differentiation is in some of the treatments at least (notably in the fertilization treatment) followed by a decrease that seems to imply a degree of return to the initial community conditions. Undisturbed plots and experimentally disturbed plots show this overall relationship but in general it appears that disturbed plots in the deserts site change less than controls, while most of the disturbances in the Mediterranean site are clearly changing to larger extents as the control.

**Relative effect of time, annual rainfall amounts, disturbance intensity and treatments (CCA results)**

In the Mediterranean site the effects of time (indicated by the sizes of effect vectors in the CCA, Figure 5a) and disturbance intensity are important determinants of community composition and structure while rainfall amount appears to be relatively of little consequence. This stands in clear contrast to the Desert site (Figure 5b) where time and rainfall amount are the main determinants and disturbance intensity is relatively less important. Fertilization treatment appears to be the most consequential treatments in the Mediterranean site (Figure 5a) as indicated by it distance to the control score. A ranking of all treatments in the order of increasing difference to undisturbed sites is: Turbation < Removal < Depression = Sealing < Input < Fertilization.

Some species are characteristic in respect to the evaluated factors. In the Mediterranean site the annual grass *Avena sterilis* is associated with increasing disturbance intensity and the shrub *Cistus salviifolius* increases with time. For the Desert site an association of the species *Trigonella stellata* with increasing rainfall stands out and over time *Stipa capensis* and *Pteranthus dichotomus* appear to become more important.

**Discussion**

Our comparative analysis of community structure and composition on undisturbed and disturbed plots demonstrates that the two climatically contrasting sites experienced over the time span of almost 20 year very distinctive patterns of vegetation dynamics. It appears that the plant communities in Mediterranean are more affected by disturbance and do not regenerate towards undisturbed conditions even after 19 years. The desert plant communities in contrast show relatively small effects and a clear trend of regeneration is visible within the studied period. Overall, this suggests a larger resilience of our desert plant community in comparison to communities found in the Mediterranean site, clearly the opposite to our initial hypothesis.

Among the separate treatments the large effects of the fertilization treatment in the Mediterranean site and the large effect of the depression treatment in the Desert site stand out. The former exemplifies the importance of nutrients in an environment that is less controlled by the lack of water. The latter is remarkable as the community that developed in the artificial depression is the only one that differed clearly from control site (see photo, Figure 6). Unlike all the other
treatments the creation of a depression ameliorates the availability of water, the main limiting resource in arid systems. Such disturbances, human or animal-made, are known to be of lasting effect (Gutterman et al. 1990, Shachak et al. 1991, Boeken and Shachak 1994, Boeken and Shachak 1998).

Do our results suggest that less arid systems indeed need much more time to recover from perturbations than more arid sites? This appears to be in contrast to general predictions that assume that arid systems are more affected by disturbance and are thus less resilient and therefore characterized by very slow regeneration or successional change. The latter view is documented by the majority of studies. This is exemplified by Polis' (1991) statement about the lack of good evidence for biologically driven processes (including succession) that occur in biotic communities of desert (the autecology hypothesis; see discussion in Holzapfel 2008). Likewise, Fowler (1986) reviewed numerous studies of vegetation change after disturbance in deserts, however states that in most cases disturbed sites are colonized by species already present in the previous communities and thus only changes in relative abundances are found. Even though Seely (1991) finds evidence for facilitative effects among plants in the colonization of desert dunes that suggest the existence of succession (sensu Connell and Slayter 1977), complete community changes as they are postulated in a series of successional series appear to be rare in deserts.

The background provided above makes a careful evaluation of our apparently contradicting results necessary. This evaluation will be related as four arguments, most of them related to the life strategies of plant communities under concern:

1. Fowler's (1986) review suggest that most desert communities do not undergo true successional change as even initial stages after disturbance are colonized by the same species that were dominant prior to impact. Our data from the Desert site agree with such view of direct revegetation. This is confirmed by Boeken and Shachak (1998), who observed recolonization of small scale disturbances in the Negev desert and showed that such patches later on even provide seed sources for surrounding undisturbed areas. However, regardless if one considers the development after perturbation in our desert site as a simple regeneration or as a true succession, as more typical for mesic environments (Odum 1959), the desert community still displays signs of greater resilience.
2. The indisputable larger resilience of our desert communities is likely related to the fact that community structure in desert is clearly related to rainfall but not to disturbance intensity while in the Mediterranean disturbance intensity is among the most important community determinants (as measured as factors in CCA). This indicates that inter-annual rainfall variation is the driving force of community change and therefore much more important than any other factor. Thus effects of disturbance are very likely masked by rainfall effects in the desert but not so in the less variable Mediterranean site. Our CCA analysis study also showed that time is important for community change in both sites. However, this seems to be driven by temporal community dynamics change due to disturbance in the Mediterranean and due to fluctuating rainfall amounts in the desert. That temporal abiotic variation between years and as pulse-driven dynamics even within years (Novoprášsky and Goldberg 2001) is an accepted paradigm for desert ecosystems (Noy-Meir 1973) that needs no further discussion here.

3. A major difference that is likely related to the larger resilience of our desert community is the fact that, in comparison to the Mediterranean site, it is dominated by annual plant species. Annuals obviously have shorter life-cycles and annual plant populations therefore are characterized by much shorter turn-over times than long-lived perennials. The annual life-form has been interpreted as an adaptation to fluctuating resources since annuals are able to survive detrimental times in seed stages (Venables and Lawlor 1980) and are capable of fast reaction to times of abundance due to fast population growth (Cohen 1966). In turn the annual life-form of desert annuals can be understood as a pre-adaptation to disturbance as well (Baker 1974) and as such will facilitate regeneration after perturbation as seen in our study. Indeed, all of the studies that show very slow secondary successions were conducted in deserts dominated by perennials. A recent analysis of the centennial study at Tamamoo Hill in the Sonoran Desert demonstrated that it took more than 50 years for the perennial vegetation to recover (Guo 2004). Interestingly this study also showed that when such long time periods are analyzed, rainfall amounts seem not to be of importance for overall succession, this even though population level changes of short-lived plants at this site were clearly driven by fluctuation in precipitation amounts (Goldberg and Turner 1986). Whittford et al. (1995) reported that desert shrubs (Larrea tridentata) showed high resilience to drought after ceasing experimental treatments but non-woody perennials did not. Likewise, Whittford et al. (2001) found in a study in the Chihuahuan Desert that perennial non-woody plants did not return 15 years after disturbance even though shrub cover was provided by planting. The statement of Lathrop and Rowlands (1983) that complete recovery of denuded sites might be in the order of centuries or even millennia clearly refers in some cases to sites with extremely long-lived and slow-growing perennials.

4. The final line of thought is related to the comparative complexity of systems under disturbance impact. As indicated by the strong difference of species richness and diversity (see Holzapfel et al. 1992) between our two sites it is clear that the desert system is much simpler and the possibilities for numerical change or re-assembly are much more limited here. While this appears to be a mere mathematical argument it is also related to the long-lasting discussion whether complex systems are more stable than less complex systems (Kikkawa 1986 and many others). In our case we can argue that the simpler desert community appears to be, or is, more stable in the face of disturbance.

Conclusion
In a detailed evaluation of the data for four years after impact that also included population data Holzapfel (1994) concluded that the dynamics in the Mediterranean site suggested the beginning of a directed succession and that the Desert site is affected by rain driven fluctuation. While now, after 20 years, time (our greatest teacher) proved the first statement to be premature, the second statement held. When testing for resilience, a concept that integrated both departure and return from original states, it appears that in our case the communities of the more arid site are more resilient than the less arid site. The apparent contradictions of this finding to a large body of literature can be understood by considering the idiosyncrasy of our studied system. As detailed above, namely the relative predominance of annual plant species in the desert site can be used to explain our results. At the same time this illustrates that a consideration of life strategies of the plant species that compose a community need to be considered when community change is studied.

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