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Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa

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Abstract The analysis of long-term floristic changes was conducted on nine west-Mediterranean limestone islands (size range: 2–95 ha) which have recently undergone a severe demographic explosion in their yellow-legged gull *Larus cachinnans* colonies. A comparison of past and present plant inventories was used to quantify extinction-colonization events, both from a classical biogeographical perspective (per island approach) and a metapopulational perspective (per species approach). In the first approach, floristic turnover intensity was negatively related to island area and positively to gull nesting density, but was independent of island isolation. In the second, species turnover rate was compared with a set of plant species life history traits (dispersal mode, Grime CSR strategy, growth form, biogeographical type). Plants which exhibited the highest turnover rate were primarily ruderal, annual, wind-dispersed species with a wide geographic range. The severe disturbance induced by seabird activities has tended to select and favour some adapted plant species groups at the expense of indigenous island taxa. The relationships between specific turnover intensity and plant life history traits justify using the metapopulation approach and point to the importance of interspecific variations in extinction-colonization patterns.

Key words Plant life history traits · Extinction-colonization · Metapopulation · Gull colonies ·*Larus cachinnans*

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Introduction

The quantitative study of species changes in natural communities has received a great deal of attention from ecologists, particularly after the publication of the dynamic equilibrium theory (MacArthur and Wilson 1963, 1967) which led to several species turnover studies. The analysis and quantification of repeated population extinctions or immigrations within ecological communities have notably been performed on island ecosystems for vertebrate (Lynch and Jonhson 1974) and invertebrate (Schoener and Spiller 1987) animal species, and for plant species (Abbott 1983; Nilsson and Nilsson 1982; Roger and Morrison 1994), although data for the latter are few.

Changes in plant communities on islands were first studied using the standard theory of island biogeography (MacArthur and Wilson 1963, 1967), addressing mainly the question of how species richness patterns can be related to island parameters like area and isolation. This model has often been criticized, as it fails to include interspecific characteristics, particularly those related to dispersal capabilities which may greatly determine the reaction of species to population size and isolation (Gilbert 1980; Ouborg 1993). To avoid these problems, some recent plant turnover studies have used the metapopulation approach (Ouborg 1993; Morrison 1997). This approach is related to the metapopulation concept (Hanski 1998) and considers an ensemble of local populations (subpopulations) assumed to be interconnected by dispersal and subject to both immigration and extinction (Levins 1969). Emphasis is then placed on extinction-colonization dynamics focusing on individual species rather than on species pool. The metapopulation approach is the per species equivalent of the classical insular biogeographical approach (Morrison 1998). Although relatively infrequent in plant studies, particularly for long-lived species, the per species approach makes it possible to consider and study between-species differences (Morrison 1997). Nevertheless, there have been very few attempts to use plant species biological attributes and ecological strategies for understanding and interpreting interspecific differences in extinction-colonization patterns, while grouping species according to functional similarities may greatly help to understand and predict plant community dynamics (McIntyre et al. 1995; Lavorel et al. 1997).

Moreover, most floristic change studies examine small islets with low species richness and and which are less subject to disturbance. Very few have focused on Mediterranean biota (Snogerup and Snogerup 1987), one of the richest areas for plant diversity on earth (Médail and Quézel 1997), and rare are those which have considered seabird-disturbed islands.

The aim of this study was to analyse quantitatively floristic changes, i.e. extinction-colonization events, on rocky Mediterranean seabird-disturbed islands over several decades based on the classical biogeographical (per island) and metapopulation (per species) approaches. We were particularly interested in investigating: (1) how island parameters (area, isolation) are related to extinction-colonization rates; (2) whether easy-to-assess plant traits [dispersal mode, growth form, CSR life strategy sensu Grime (1977), biogeographical type] can be related to species turnover intensity, and (3) if a colonial seabird demographic explosion is likely to have driven the floristic changes.

Materials and methods

Study area and island variables

This study was conducted on nine rocky limestone islands in the Bay of Marseille, Mediterranean Sea, south-east France (approximately 43°15' N, 5°20' E). The surface area of the surveyed islands ranged between 2 and 95 ha, totalling approximately 345 ha. The distance from islands to the continent varied from 50 to 3800 m. Topography was very uneven: Riou Island (90 ha) culminates at 191 m above sea level (a.s.l.) while Plane Island (15 ha) is only 22 m a.s.l. Island area, distance to the continent and isolation (distance to the continent or to larger islands for islets close to larger islands) are given according to Médail and Vidal (1998). These islands were isolated from the mainland during the last marine transgression, circa 8000–9000 BP (Sartoretto et al. 1996). The local Mediterranean climate is quite harsh: rainfall is about 350 mm per year with a pronounced summer drought period and there are more than 200 days of high wind per year (Douguedroit 1983). These islands are covered with a low vegetation, essentially a mosaic of Mediterranean matorrals with *Pistacia lentiscus*, *Rosmarinus officinalis*, *Coronilla juncea*, *Lavatera arborea* and xeric or haline grasslands with a high proportion of bare ground and rocky patches.

The studied islands currently house one of the largest yellow-legged gull *Larus cachinnans* (Pallas) colonies in the world. As in other colonies in the Mediterranean area (Bosch et al. 1994), this colony has undergone a very severe demographic explosion since the last decades due to anthropogenic factors. From approximately 100 pairs in 1920 and 3000 pairs in 1960, the breeding population now represents nearly 18,000 nesting pairs all around the islands, with local densities sometimes exceeding 200 pairs ha^{-1} (Vidal et al. 1998a).

Survey techniques

Floristic change studies encounter several problems, particularly in Mediterranean habitats, primarily due to the difficulties in performing exhaustive plant species inventories (high species richness, presence of annuals, transient and difficult-to-detect species), which must be overcome before reliable results can be obtained (Abbott 1983). In fact, most plant species studies focus on floristic changes over a short period, generally 1–5 years (Nilsson and Nilsson 1982; Morrison 1997). In this case, surveys are generally performed by the same researcher, using a single inventory method, at the same time period each year. Long-term studies, i.e. for more than 10 years, have occasionally been performed (e.g. Herwitz et al. 1996) but are rare because (1) they require good-quality past inventories and (2) they are subject to several possible sources of artefact, including sampling errors (Nilsson and Nilsson 1982, 1983; Wright 1985). To assess the nature and intensity of floristic changes we established current plant inventories and compared them with past ones. The flora of the nine study islands was thoroughly studied and surveyed in the past by Laurent and Deleuil (1938) (Ratonneau and Pomègues Islands) and Knoerr (1960) (Riou, Maïre, Jarre, Plane, Jarron, Tiboulen and Grand Congloué Islands). The present survey techniques were strictly modelled on those used for the previous inventories, i.e. the new surveys were performed over several years (1995–1997), with year-round field work sessions. Each island and each habitat type was surveyed in its entirety, even in its least accessible areas. Field surveys entailed more than 1500 man-h, i.e. more than 4 man-h ha^{-1}. The obsolete taxonomic nomenclature used in the past inventories was corrected according to Kerguélen (1993), as were some misidentifications. In some cases, additional specific research was conducted for plant species known to have been present in the past surveys but which were absent from the initial present-day samplings.

Nesting gull density on each island was estimated by extrapolation from counts conducted on 171 systematic sampling plots set up all around the archipelago (Vidal 1998) using a method adapted from Thompson and Rothery (1991).

Quantification of plant species extinction-colonization

Relative species changes in this study were calculated using the following formula (Morrison 1997, 1998): relative change (expressed in % yr^{-1}) $S_r=[(I+E)/t(S_1+S_2)]\times100$. In the classical biogeographical approach (per island approach), E and I are the number of species extinctions and species colonizations, respectively, occurring between two surveys separated by t years. S_1 and S_2 are the number of species on each island in the first and second census. In our case, nine islands were considered with t=59 years for Pomègues and Ratonneau Islands and t=36 years for Riou, Jarre, Maïre, Plane, Jarron, Tiboulen and Grand Congloué Islands.

In the per species approach, E is the number of islands on which a species was present only in the first census and I is the number of islands on which a species was present only in the second census. S_1 and S_2 are the number of islands on which a species was present both in the first and second censuses, respectively. In this approach, we eliminated Pomègues and Ratonneau Islands and only studied the seven islands which had been surveyed at the same period, both in the past (Knoerr 1960) and in the present study. Although the aim of this study was not to test the metapopulation structure of the island floras, the seven study islands are located very close to one another, which makes plant dispersal within the island network both possible and plausible. At the very least, the largest islands may act as a source of propagules for smaller populations on nearby islets, according to the stepping-stone island theory (Carlquist 1965).

Plant biological traits

Each plant species was characterized by four biological traits: dispersal mode, CSR strategy, growth form, and biogeographical type.

Seed dispersal modes were separated into six categories adapted from Van der Pijl (1982). For each species, we assessed a main dispersal type using data from Molinier and Müller (1938) complemented by personal observations. The six categories were: plumed diaspores (light anemochorous: Lanem), winged diaspores and tumbleweeds (heavy anemochorous: Hanem), long-distance zoochorous seeds (i.e. epizoochorous, synzoochorous and endozoochorous: Zooch), myrmecochorous (Myrm), hydrochorous (Hydr), or no special long-distance device (Nosp), including barochorous and ballistic species.

Plant strategies were examined according to the CSR model proposed by Grime (1974, 1977) except for the stress tolerance interpretation (see below). Three sensu lato strategies were taken into account: (1) competitive species, i.e. species with dominant competitive ability (C s.l. strategy: C+CR+CS) which presented high vegetative development, ecological plasticity and occasionally some allelopathic potential; (2) ruderal species, i.e. species with a prevalent tolerance to disturbance (R s.l. strategy: R+RS+RC) living in frequently disturbed habitats and which showed a high growth rate, short life cycle and high seed production; (3) dominantly stress tolerant species (S s.l. strategy: S+SR+SC) which can be encountered in harsh habitats characterized by ephemeral and unpredictable resources. In the strict Grime sense, one of the most crucial traits of stress-tolerant species was slow growth. However, for annuals species, we have followed the conceptions of Madon and Médail (1997) who have demonstrated that these plants could suit two different strategies under the Mediterranean bioclimate: in xeric habitats with low resilience, annuals are mainly stress tolerant, whereas in productive and disturbed habitats they correspond to the ruderal strategy.

Seven growth form categories were considered based on Raunkiaer's (1934) classification amended by Ellenberg and Mueller-Dombois (1967): therophytes (Th), biennial hemicryptophytes (Hb), perennial hemicryptophytes (Hv), geophytes (G), chamaephytes (Ch), nanophanerophytes (NP) and phanerophytes (P).

Each plant species was classified biogeographically according to Pignatti (1982) and Gamisans and Jeanmonod (1993): endemic and subendemic taxa (End s.l.), taxa restricted to the Mediterranean coast, i.e. steno-Mediterranean species (StenoM), taxa whose range is centred around the Mediterranean area, i.e. eury-Mediterranean species (EuryM), Irano-Turano-Mediterranean, Mediterranean-Atlantic, sub-Atlantic or south-European taxa (Med s.l.), Eurasian, boreal, subtropical, European or cosmopolitan taxa (Cosm), non-indigenous and planted taxa (Xeno).

Comparison of the distribution of plant biological traits between the zero-and maximum-turnover species set was tested with the χ^2-test (Scherrer 1984).

Results

Per island approach

The annual relative extinction-colonization rate (S_r) varied from 0.469% year^{-1} for Ratonneau Island to 1.187% year^{-1} for Tiboulen Island. S_r was strongly correlated with the portion represented by newly established plant species (r^2=0.885, P<0.001; Fig. 1A), but no correlation was found with the proportion represented by extinct plant species (r^2=0.084, n.s.).

The annual relative extinction-colonization rate was negatively correlated with island area (r^2=0.752, P<0.005; Fig. 1B) and positively correlated with gull nesting density (r^2=0.649, P<0.01; Fig. 1C). However, no significant relationship was found between annual relative extinction-colonization rate and distance from the continent (r^2=0.017, n.s.) or with isolation (r^2=0.312, n.s.).

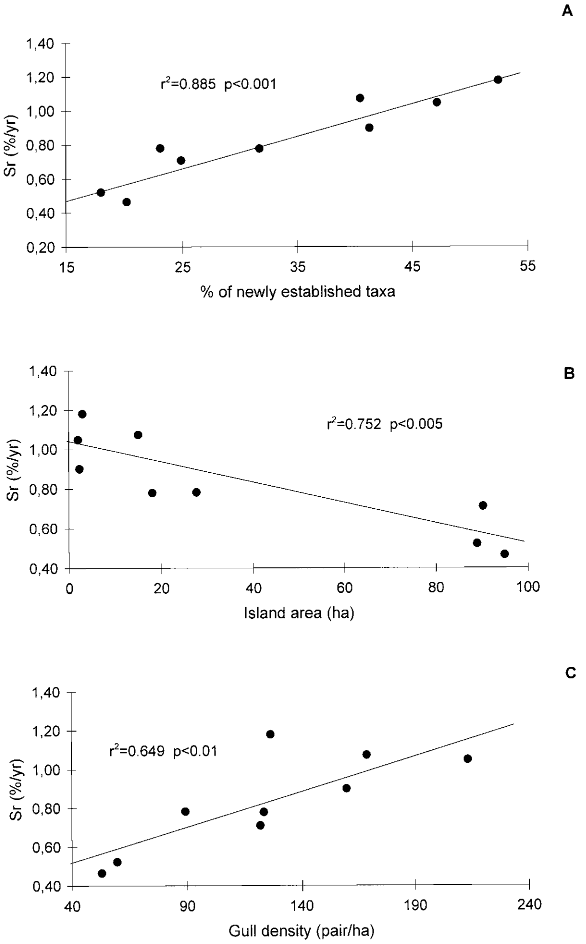

Fig. 1 Relationships between the relative extinction-colonization rates on islands and some variables relative to the islands [values of S_r (% year^{-1}) for the Marseille islands (islands by decreasing area): Ratonneau 0.469, Riou 0.787, Pomègues 0.509, Maïre 0.809, Jarre 0.940, Plane 1.067, Jarron 0.820, Tiboulen 1.187, Grand Congloué 0.893]. **A** Relationship with the proportion of new plant species in the total island flora. **B** Relationship with island area. **C** Relationship with the mean nesting gull density on each island

Per species approach

Due to the low number of islands considered (seven), extinction-colonization rates calculated on a per species basis showed 17 different values from 0% year^{-1} (species which have not undergone any extinction or colonization event, i.e. 'zero-turnover species') to 2.703% year^{-1} (species which have undergone extinction on all the islands where they were recorded in the first census and/or which were absent from the first census on islands where they were recorded in the second, i.e. 'maximum-turnover species'). The distribution of species was not uniform and the total for the two extremes (zero and maximum turnover) was more than 60% of the whole species set (24.1% for S_r=0 and 36.1% for S_r=2.703; Fig. 2). This essentially bimodal strength distribution between the two extreme values of S_r led us to compare the distribution of life history traits between zero- and maximum-turnover species sets.

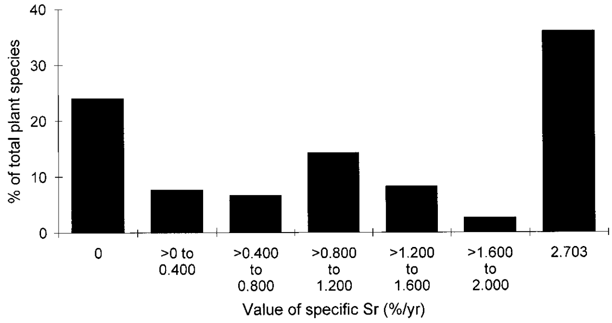

Fig. 2 Distribution of island plant species strength among the different values of relative extinction-colonization rates

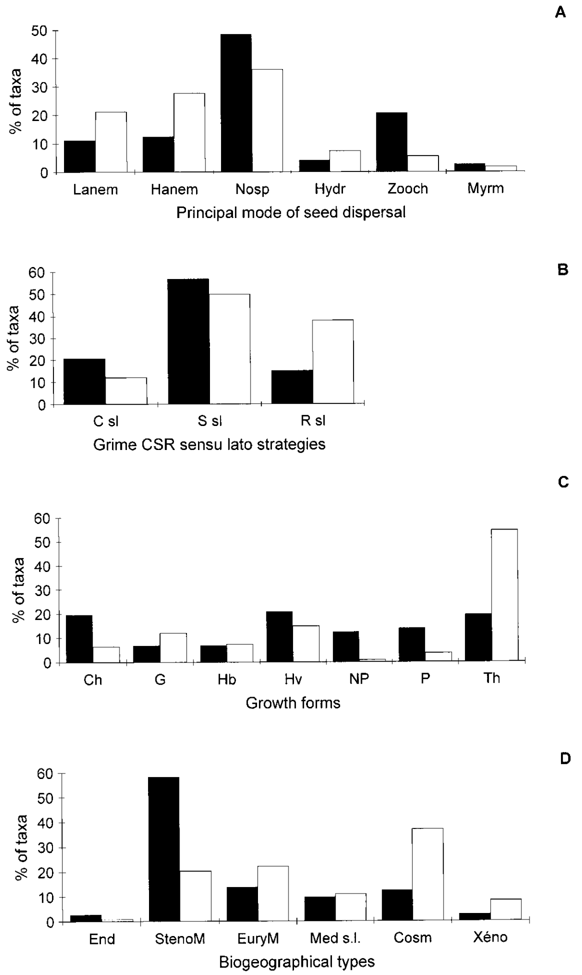

Fig. 3 Comparison of plant biological traits between zero- and maximum-turnover species sets (*black bars* zero-turnover species, *open bars* maximum-turnover species). See Materials and methods for explanation of abbreviations. **A** Modes of seed dispersal. **B** Grime CSR sensu lato strategies. **C** Growth forms. **D** Biogeographical types

Zero/maximum-turnover species

Zero- and maximum-turnover plant species showed significantly different dispersal modes ($\chi^2=18.45$, $df=5$, $P<0.005$; Fig. 3A), but both exhibit a high rate of no special long-distance device. Maximum-turnover species were generally dispersed by wind but more rarely dispersed by animals compared to zero-turnover species.

Zero- and maximum-turnover plant species showed significantly different Grime CSR sensu lato strategies ($\chi^2=10.18$, $df=2$, $P<0.01$; Fig. 3B). Overall, R s.l. strategy taxa are rarer among zero-turnover species than among maximum-turnover species while C s.l. strategy taxa show a higher percentage of zero-turnover species than maximum-turnover species. The S s.l. strategy is roughly equally represented among zero- and maximum-turnover species.

The growth forms of zero- and maximum-turnover species were also significantly different ($\chi^2=37.63$, $df=6$, $P<0.0001$; Fig. 3C). Zero-turnover species differed from total-turnover species in four main points: there was a clear predominance of lignous plants (chamaephyte, nanophanerophyte, phanerophyte taxa) and, to a lesser extent, hemicryptophyte taxa. Maximum-turnover plant species were clearly dominant among therophyte species and occasionally among geophytes.

Zero- and maximum-turnover species were also significantly different from a biogeographical perspective ($\chi^2=31.80$, $df=4$, $P<0.001$; Fig. 3D). Zero-turnover species were more strictly Mediterranean, while maximum-turnover species were more frequently cosmopolitan or xenophyte species, but also eury-Mediterranean plants.

Discussion

Per island approach

The fact that turnover intensity was shown to be strongly correlated with the percentage of immigrant species but independent of the percentage of extinct species suggested that the floristic changes which have occurred have been caused by the massive establishment of new species rather than the extinction of pre-existing taxa. In fact, the current flora on most of the islands contains a large number of newly established plant species (up to more than 50% of the total plant species on Jarron Island; Vidal et al. 1998a, 1998b).

The intensity of floristic changes for the nine islands considered was much lower than the turnover rates usually observed for vascular plant species, i.e. 1–10% year^{-1} (see Schoener 1983 for a review). However, the islands considered in Schoener's review were smaller than those of the Bay of Marseille and thus more subject to high variations in environmental conditions, particularly catastrophic events. As shown by MacArthur and Wilson's (1967) biogeographical theory, extinction-colonization rates are inversely related to island surface area. This concurs with the results of Nilsson and Nilsson's (1982) island plant studies on Lake Möcklen, but differs from those of Abbott and Black (1980) on Australian islets. Plant extinction-colonization rates on Marseille islands were demonstrated to be independent of isolation as in Nilsson and Nilsson's (1982) studies, as opposed to MacArthur and Wilson's (1967) predictions. The very low isolation (maximum 3100 m) of the studied islands may be the reason for the non-isolation-related effect, as has already been shown for plant composition on large groups of islands in the same geographic area (Médail and Vidal 1998). The present study also demonstrated a positive correlation between gull nesting densities on islands and turnover rates. The fact that floras on islands with seabird colonies generally tend to have higher extinction and immigration rates than those on islands without bird colonies is well established and has often been related to propagule dispersal by seabirds and the creation of disturbance patches by trampling and manure (e.g. Dean et al. 1994).

Per species approach

Distribution of species strength within turnover values

One of the outstanding results revealed by the per species approach is that almost two-thirds of the species found on the surveyed islands showed one of the two extreme species turnover values. This statement leads to two conclusions.

First, despite the long time period between the two surveys and the severe environmental changes, a large number of plant species have resisted extinction and, as yet, have not colonized other islands. Moreover, the zero-turnover plant species group includes both taxa distributed over most (sometimes all) of the studied islands and taxa restricted to only one of the islands considered.

Second, a larger group of plant species has systematically altered their presence/absence status on all the islands (i.e. sub-populations) where they were recorded. This may be due to two combined factors: first, yellow-legged gulls now nest on all the islands studied and their mean densities are always high (minimum :52.8 pairs ha^{-1} on Ratonneau Island). Thus, in spite of their very different seabird densities, all the islands now exhibit gull-disturbed habitats, prone to the establishment of new plant species, and the pressure of gull activities is sufficient to exclude some unadapted species. Second, the distances between islands and distance from the mainland are short, which reduces isolation as a selective factor for immigrant species (Vidal et al. 1998b).

Despite our efforts and precautions in generating a current island plant inventory, our lists no doubt include some errors. Some of the turnover illustrated may be pseudoturnover caused by sampling difficulties (Nilsson and Nilsson 1983, 1985). For instance, some plant species present in the soil seed bank may not have germinated during the census period. Nevertheless, we assume that the portion represented by pseudoturnover in the total true turnover was very low because the inventory period was spread out over more than 24 consecutive months.

Relationships between specific turnover rate and species life history traits

The significant differences between dispersal mode in zero-turnover species compared with maximum-turnover species justified using the metapopulation approach because it includes species-specific differences. This result contrasts with those from Nilsson and Nilsson (1982) which demonstrated no clear difference in colonization-extinction rates between the different dispersal modes. The fact that an important number of plant species, both among zero- and maximum-turnover species, shows no special long distance dispersal device, supports the theory that dispersal capabilities between nearby islands, i.e. the potential dispersal distance, is not a determinant factor for specific turnover intensity. The predominance of the 'no special device' class is also consistent with Willson (1993) who indicated that many plants have 'no evident morphological adaptation for dispersal'. The very low number of zoochorous taxa, notably among the taxa which have recently colonized the whole island group indicates that yellow-legged gulls are not good dispersal agents, despite their daily movements between the islands and the mainland (Vidal et al. 1998b). In contrast, several cosmopolitan plant species with small seeds can be found on gull nesting or resting areas (Vidal 1998). This situation is different from that in gull colonies in other parts of the world (Gillham 1956; Hogg and Morton 1983; Morton and Hogg 1989), probably because the yellow-legged gull is an essentially flesh-eating detritivorous bird which now essentially feeds on rubbish dumps and trawling discards but more rarely in natural environments (Bosch et al. 1994).

If we consider Grime's CSR strategies (1974, 1977), competitor plants can grow on productive, but relatively undisturbed and stable habitats. The present results concur with this pattern as the C strategy is mainly associated with zero turnover. In productive and frequently disturbed habitats, the ruderal strategy is favoured due to the high relative growth rate and early onset of flowering which induce rapid population fluctuations. This explains the predominance of total turnover among these ruderal species which quickly grow on disturbed patches created by gulls (Vidal et al. 1998b). The predominance of stress-tolerant plants among zero- and total-turnover species reflects the ecological bivalence of this strategy which includes both long-lived evergreen shrubs with quite low population fluctuations, and annual plants with high turnover (Madon and Médail 1997).

It has already been demonstrated that therophyte species have a higher species turnover rate than other plant life forms due to their variable population fluctuations, and this pattern occurs on different types of islands (Snogerup and Snogerup 1987; Robinson et al. 1994; Herwitz et al. 1996). Thus, the prevalence of therophyte species among maximum-turnover species compared with zero-turnover species is not surprising. Our results are similar to those of Herwitz et al. (1996) who found that annual forbs had the highest species turnover rates followed by grasses and perennial forbs. In fact, therophytes are known to flourish on rookeries, particularly in the open patches created by habitat destruction by colonial seabirds (Gillham 1956; Sobey and Kenworthy 1979; Hogg and Morton 1983). Moreover, therophyte species typically represent a large number of the invasive plants in the world, particularly in the Mediterranean basin (Quézel et al. 1990).

The high prevalence of maximum-turnover species among geophytes is more difficult to explain because bulbs generally represent a stable element in plant communities and persist in undisturbed habitats (McIntyre et al. 1995). Nevertheless, as in our case, moderate levels of disturbance are not always harmful to geophytes. As emphasized by some authors (Snogerup and Snogerup 1987), recent establishment and extension of *Allium commutatum*, a Mediterranean sea-dispersed islet specialist, is a striking example of geophyte extension on several studied islands.

Woody species (phanerophytes, nanophanerophytes, chamaephytes, climbers) mostly show a zero or a low turnover (Robinson et al. 1994; Herwitz et al. 1996). In fact, these perennial growth forms are generally deep rooted, and have been shown to be less subject to turnover, or at least to extinction, than shallow-rooted species, such as annual herbs (e.g. Quintana-Ascencio and Menges 1996). Their longer average lifespan and their better resistance to some moderate disturbance may also explain their higher persistence between the two surveys.

The predominance of maximum turnover among cosmopolitan and invasive plants on Marseille islands reflects the general life history traits characterizing these species (Williamson 1996). As in Robinson et al. (1994), the total number of non-native plants has increased over several decades. Herwitz et al. (1996) also emphasized the role of xenophytes in modifying island turnover rates. Indeed, several common traits shared by these invasive plants (R strategy, annual growth, anemochory) can partly explain the trends observed between the two censuses on Riou archipelago. Steno-Mediterranean plants, which constitute the true autochthonous floristic elements of this area, exhibit a predominant zero turnover, which concurs with the high adaptability of these plants to the harsh Mediterranean insular environments.

Influence of seabird disturbance on floristic changes

Colonial seabirds can exert a high pressure on ecosystems and influence plant community patterns and dynamics, particularly on islands, which are both very vulnerable to disturbance and often house large seabird colonies (Sobey and Kenworthy 1979; Dean et al. 1994). For instance, large yellow-legged gull colonies have greatly influenced the dynamics, composition and organization of Mediterranean island biotic communities (Vidal et al. 1998a, 1998b, 1998c). Seabird activities have several direct and indirect consequences for plant communities due to both physical disturbances and chemical changes (Gillham 1956; Hall and Williams 1981). Dense seabird colonies are notably often responsible for strong enrichment of soil nutrients and organic matter through guano and organic refuse deposition (Iason et al. 1986; Wainright et al. 1998). In the particular case of the Marseille islands, yellow-legged gulls have transferred much nitrogenous and phosphorous compounds to the soil (Vidal 1998). Soil concentrations of P were five to ten times higher for places with dense gull colonies than in those without nesting gulls, while N and organic matter concentrations increased two- to fourfold due to gull colonies. This strong soil enrichment is likely to have favoured the establishment and extension of ruderal plant species to the detriment of stress-tolerant indigenous taxa. Moreover, the creation of open stripped areas by seabirds trampling and sitting could have induced and accelerated the new establishment of allochthonous weeds (Kotanen 1997).

However, we have to keep in mind that factors other than seabird colony expansion could have influenced the floristic changes, such as polluted sea sprays, visitor impact or changes in species composition of the mainland (a potential seed source for the islands). Nevertheless, we assume that the strong yellow-legged gull demographic explosion represents the major and the most drastic change in environmental conditions to have taken place on the Marseille islands between the two surveys.

Conclusions

Finally, we must underline that the biogeographic and the species trait approaches are not independent because island parameters (notably area) are critical in regulating ecosystem functions depending on plant species ecological attributes (Wardle et al. 1997). In our case, gull densities on the studied islands (and thereby the potential predominance of certain plant traits) are negatively correlated with the island area and, thus, small islands are subject to a higher seabird disturbance pressure than large islands and are more likely to house plant species favoured by disturbance.

As shown in this study, plant turnovers can be interpreted through a relatively simple set of biological characteristics, although autocorrelation between traits is a common feature in plant ecology (e.g. Lavorel et al. 1997; Smith et al. 1997).

In this context, an integrated classification of traits (with more selected attributes) using the functional group approach (e.g. Lavorel et al. 1997; Smith et al. 1997) would be useful to (1) examine the overall responses of insular communities to severe disturbances induced by vertebrates and (2) compare the organization of plant communities between the studied islands and the nearby mainland.

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