Contrasted Successional Trajectories in a Mediterranean Wetland Due to Geomorphic- and Human-Induced Perturbations

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Abstract

Wetland ecosystems in water-limited environments locally boost biotic interactions, habitat diversity, and species concentrations, but little knowledge exists on their long-term functioning and susceptibility to regime shifts that might influence conservation and reclamation actions. Here we used a historical ecology approach on a rare Mediterranean peat-bog to reconstruct ecological successions for the last 4 millennia. The reconstruction is used to explore the role of geomorphic thresholds, climate changes, and anthropogenic perturbations as drivers of the ecosystem trajectory in the frame of the projected aridification of the climate. Our findings highlight how the superimposition of pastoral disturbances to river incision, has exacerbated ecosystem sensitivity to climate changes. Considering the long-term trajectory, the disappearance of the ecosystem might occur independently of changes in the precipitation regime. Insights given by Historical Ecology have implications for our understanding of ecosystem responses to perturbations, demonstrating that long-term dynamics must be considered before engaging in strict conservation action.

Key words: ecological succession; ecological functioning; paleoecology; wetland; island; Mediterranean.

Highlights

- Ecosystem successions of a Mediterranean wetland are analysed for the last 4 kyrs.
- The Baglietu peat-bog (Corsica, France) is investigated using Historical Ecology.
- Geomorphic-induced threshold exacerbated ecosystem sensitivity to climate changes.

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Introduction

Wetlands located in water-limited environments are vital to temper dryness (D'Odorico and Bhattachan 2012). Through water retention and carbon storage, these wetlands boost, locally, a variety of abiotic and biotic interactions, favouring a diversity of habitats, and a formidable concentration of species (Dudgeon and others 2006; Maestre and others 2012; Tooth and others 2018). In the Mediterranean basin, wetlands represent only 1.5% of the land surface but host about 30% of the vertebrate species (Mediterranean Wetland Observatory 2018). These habitats act as drought refuges for numerous species (Robson and others 2011) by mitigating water stress induced by the irregularity of precipitations (Zacharias and Zamparas 2010). While having high ecological values, Mediterranean wetlands are exposed to major stressors. Land reclamation for agriculture, cattle grazing, infrastructure construction, vegetal resources exploitation, have been historical drivers of surface reduction and drainage of wetlands (Junk and others 2013). The evolution of geomorphic configurations (for example, disconnection from river systems and aquifers, rising sea levels) driving changes in hydrology, salinity, and alkalinity, together with climate aridification are expected to induce a shift to drier habitats during the twenty-first century (Koutroulis 2019), that will be superimposed on human-induced ones, likely triggering losses in biological diversity, ecological functions and ecosystem services (MedECC 2020).

Enhanced awareness of wetland ecosystem functions, fostered by the implementation of the Ramsar Convention in the Mediterranean (Geijzendorffer and others 2019) remains, however, insufficient to ensure their protection. About 50% of these habitats have been lost through the twentieth century (MedECC 2020), and some ecological communities, such as aquatic insects are poorly addressed (Tierno de Figueroa and others 2013). As an example, in Italy, only two freshwater beetles are included in the Conservation of Natural Habitats and Wild Fauna and Flora Directive, one of them (*Dytiscus latissimus*) being almost certainly extinct and the other, (*Graphoderus bilineatus*) not having been observed for the past few decades (Trizzino and others 2013). Thus, there is an urgent need to improve our understanding of Mediterranean freshwater wetlands ecological functioning and drivers of evolution, in particular by including insect communities (McDermott 2021).

The purpose of the study is to explore the driving factors modulating long-term ecological functioning and biodiversity of wetlands located in water-limited environments, and how this knowledge can help to adjust conservation efforts. We use the Historical Ecology approach (Willis and others 2010; Barnosky and others 2017; Poher and others 2017) to the 2.4 m-thick deposit of the Bagliettu peat-bogs, one of the only two hygro- to meso-hygrophilous zones of the Corsica Island located in the dry sub-humid Mediterranean: (1) to reconstruct 3900 years of insect and plant ecological successions and changing habitats, (2) to identify respective and cumulative roles of past disturbances (that is, geomorphic evolution, climate changes, land use) in the shaping of ecological communities, and 3) to discuss conservation status in the light of the long-term dynamics.

Study Area

Bagliettu (42° 28′ 54″ N, 09° 11′ 17″ E, 210 m a.s.l.) is a peat-bog measuring 17 hectares, located on the left bank of the inherited floodplain of the Asco river (Figure 1), that drains a mountain catchment of 365 km^2 reaching altitudes of 2700 m. The Asco hydrological regime is characterized by a seasonality of water discharge that echoes a seasonality of the temperatures and precipitations (mean of respectively + 5.5 °C/70 mm in winter, and + 22.5 °C/20.5 mm in summer). Flood generation occurs mainly in autumn and in spring, while summers are marked by high evapotranspiration. Although restricted to a steep and narrow channel upstream, the river evolved in a braided-style, 10 km-wide, and 2% steep alluvial plain from about 300 m a.s.l. where two peatlands have developed, including Bagliettu (Figure 1). Part of the peat-bog dries up in summer, but humidity persists throughout the year in its lower part (DREAL 2010-11). Hydrochemical analyses carried out in the other peat-bog of the valley (Valdu 250 m a.s.l.) show that the water table remains stable over the year (Santoni and others 2021). River flow and rainwater contribute the most to the aquifer recharge, but it is a low perennial inflow coming from the slope that maintains the water table high enough to keep the peat-bog connected during the driest months.

Bagliettu is located within the meso-Mediterranean vegetation level (Figure 1), but 70% of the flora correspond to circumboreal and eurosiberian taxa (Gamisans and others 1998). The phytosociological communities are structured by the proximity to the riverbed (Gamisans and others 1998). The acid oligotrophic river habitat is typically characterised by a floating stratum rich in *Potamogeton*

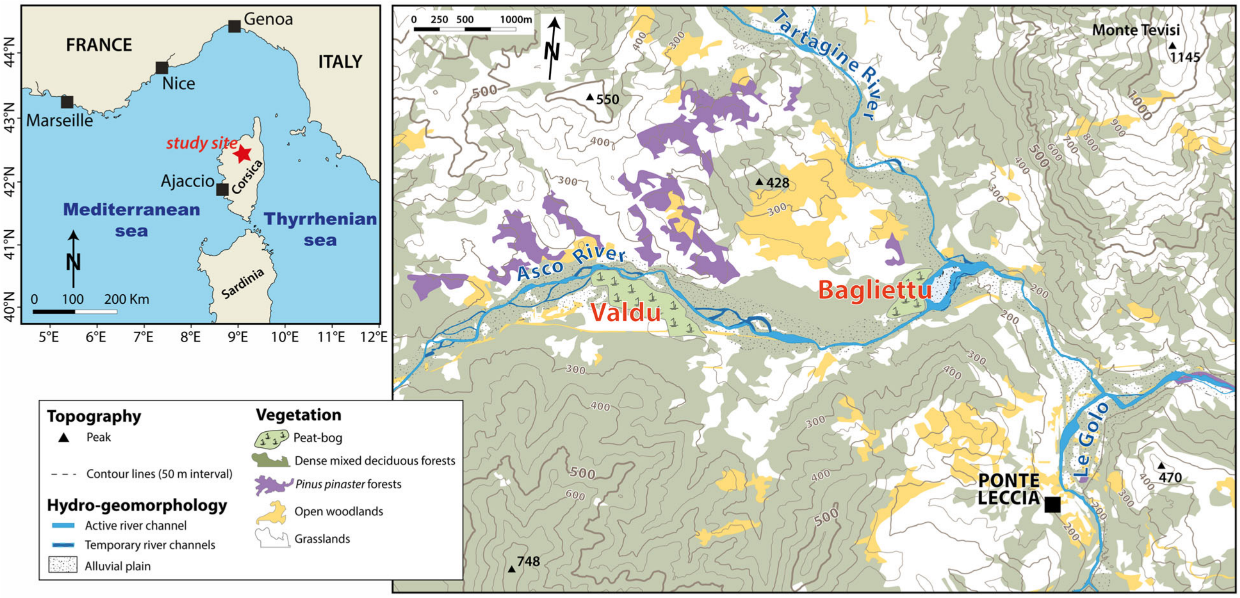

Figure 1. Location map of the study site, in the sub-humid dry Mediterranean region. The wetland of Bagliettu is situated on the left bank mountain river of Asco, perched at 1.5 m above the active channel, at 210 m a.s.l. The area is situated in the meso-Mediterranean vegetation stage dominated by a mixed deciduous forest on the north-facing slopes while south-exposed flanks are covered by xeric shrub and grasslands.

polygonifolius accompanied by *Callitriche stagnalis*. They develop under shade brought by *Alnus glutinosa*. Amphiphytes and helophytes as *Ludwigia palustris, Mentha aquatica, Helosciadium nodiflorum,* occupy the smoother riverbanks. Alder groves develop on the Asco riverbanks, and the alder riparian forest is characterized by a tree stratum dominated by *Alnus glutinosa*, together with *Fraxinus ornus* and *Salix cinerea.* The herbaceous strata are dominated by *Rubus ulmifolius*, *Pteridium aquilinum*, *Hypericum hircinum*, *Eupatorium cannabinum* subsp. *corsicum*, *Osmunda regalis*, and *Ranunculus lanuginosus.* At about 1.5 m-high above the river bed, peaty depressions are favourable to the development of hydrophyte species of *Potamogeton polygonifolius* associated with *Juncus bulbosus* and *Thelypteris palustris*. The peat mounds are topped by a dense vegetation composed of several strata: (1) a tree stratum (*Salix atrocinerea*, *Frangula alnus*, *Alnus glutinosa*, *Betula pendula)* develops on the peat-bog edges, (2) a dense shrub layer, dominated by *Erica terminalis* of about 1.5 m high, (3) an herbaceous stratum made of species belonging to various phytosociological classes (*Scheuchzerio palustris-Caricetea fuscae*, *Agrostietea stoloniferae* and *Phragmiti australis-Magnocaricetea elatae*). Within these herbaceous communities, exist several rare or protected orchids (*Liparis loeselii, Platanthera algeriensis, Spiranthes aestivalis*; Table 1), as well as the carnivorous plant *Drosera rotundifolia* (Table 1). The peat surface shows incision trails caused by cattle trampling. A swampy alder forest with *Malus sylvestris*, *Rosa sempervirens* and *Phillyrea latifolia* occupies the highest parts, associated with hygrophilous plants.

Material and Methods

Four sediment cores were sampled with a Russian Corer (Ø = 8 cm) in June 2014 in the Bagliettu peat-bog, among the *E. terminalis* stands. The neighbouring peat-bog of Valdu was also cored, but the exceedingly thin nature of the deposit and the density of tree roots make this site inappropriate for a Historical Ecology approach. The analyses were carried out at the Institut Méditerranéen de Biodiversité et d'Écologie (France). Based on sedimentological descriptions (texture, colour, grain size, macroremains presence) and core correlation, a 240 cm-long sediment sequence was built. The entire sequence was sliced every 5 cm, resulting in 97 samples of a constant volume of 83 cm^3. Plant macrofossils (size > 300 μm) were sorted, and insects were extracted using the standard paraffin flotation method (Coope 1986).

Identifications of Coleoptera and Hymenoptera: Formicidae were made by direct comparison with specimens from the modern reference collection of the Institut Méditerranéen de Biodiversité et d'Ecologie (France). Trichoptera were identified using Lepneva (1964–1971) and Faessel (1985)'s

Table 1. List of the Remarkable Plant Species of the Bagliettu Peat-Bog

Scientific name	Family	Status	Rarity	Regional IUCN status
Drosera rotundifolia L. R.*	Droseraceae	NP	RR	
Frangula alnus Mill. subsp. *alnus*	Rhamnaceae	PI	RR	NT
Kickxia commutata (Rchb.) Fritsch subsp. *communata*	Plantaginaceae	NP	C	LC
Liparis loeselii (L.) Rich	Orchidaceae	NP	RR	CR
Listera ovata (L.) R. Br	Orchidaceae	PI	IF	
Ophioglossum vulgatum L	Ophioglossaceae	PI	R	LC
Persicaria hydropiper (L.) Delarbre	Polygonaceae	PI	R	LC
Platanthera algeriensis Batt. & Trab	Orchidaceae	PI	R	LC
Ranunculus macrophyllus Desf	Ranunculaceae	NP	IF	LC
Ranunculus ophioglossifolius Vill. R	Ranunculaceae	NP	C	LC
Spiranthes aestivalis (Poir.) Rich	Orchidaceae	NP	IF	LC
Thymelaea tartonraira subsp. *thomasii* (L.) All	Thymelaeaceae	RP	IF	NT

*NP national protection, RP regional protection, PI patrimonial interest, Rarity status: RR, very rare, R, rare, IF infrequent, C common; IUCN categories according to Delage and Hugot (2015): CR critically endangered, NT near threatened, LC least concern. The nomenclature and the rarity status of the species are quoted according to Jeanmonod and Gamisans (2013). *Introduced species.*

Table 2. Results of the AMS Radiocarbon Dates (Bagliettu, Corsica)

Laboratory code	Depth (cm)	Material (seeds, fruits, buds)	Age ^{14}C BP	Calibrated age at 2σ (cal. BP)
Poz-74273	50–55	*Alnus*, *Carex*, Euphorbiaceae, *Moehringia*, *Potentilla*, *Rubus*, *Vitis vinifera*	475 ± 30	498–540
Poz-80365	70–75	*Alnus*, *Carex*, *Moehringia*, *Rubus*, *Sambucus*, *Vitis vinifera*	1375 ± 30	1268–1339
Poz-80366	80–85	*Carex*	2815 ± 35	2800–3020
Poz-74201	90–95	*Alnus*, *Carex*, *Potamogeton*	2835 ± 35	2859–3057
Poz-74274	140–145	*Alnus*, *Carex*, *Mentha*, *Moehringia*, *Rubus*, *Sambucus*	3190 ± 30	3362–3458
Poz-74275	185–190	*Alnus*, *Carex*, *Hypericum*, *Rubus*, *Sambucus*	3435 ± 35	3595–3827
Poz-74202	220–225	*Carex*, *Rubus*	3420 ± 35	3578–3823

work. The Minimal Number of Individuals (MNI) for each insect taxon was estimated by counting diagnostic elements of the exoskeleton (Supplementary Material 1–2). Insect nomenclature follows Tronquet (2014) for Coleoptera and Fauna Europaea for the other orders. Insect taxa were merged into meaningful ecological groups (Supplementary Material 3) according to the BugsCEP database (Buckland and Buckland 2006) and the literature for the Mediterranean region (Caillol 1908–1954; Sainte-Claire Deville 1914; Thérond 1975–1976).

The nomenclature of vascular plants follows *Flora Corsica* (Jeanmonod and Gamisans 2013) and the phytosociological scheme is based on the *Prodrome des végétations de Corse* (Reymann and others 2016). Plant remains were identified using the reference collection of the Institut des Sciences de l'Évolution de Montpellier (France), and European atlases (Schoch and others 1988; Cappers and others 2012). Seven plant macrofossil samples were selected for radiocarbon dating (Poznań radiocarbon Laboratory). The ^{14}C ages (Table 2) were calibrated at a 95% interval of confidence using the Intcal20 calibration curve (Reimer and others 2020). The age-depth model was built using the Clam R package (Blaauw 2010). The samples represent between 30 and 80 years.

A depth-constrained hierarchical cluster analysis (CONISS algorithm) in the Rioja R package (Juggins 2012) was used to define the statistically homogeneous Insect Assemblage Zones (IAZ) and Plant Assemblage Zones (PAZ). Ecologically, groups expressed in abundance, were transformed into influx (number of remains per volume and per interval of time) to normalise effects of changing sediment accumulation rates, and a resampling applied (bins of 100 years) to standardise changes in temporal resolutions, to prevent misinterpretation in terms of ecological dynamics. This results in a homogenized dataset of 39 individuals (that is, time window of 100 years) and 9 ecologically meaningful variables (that is, dung, decayed matter, meadow, woodland, riparian, scrubland, aquatic, leaf-trees, diversity). A Principal Component Analysis (PCA) was performed to ordinate the individuals into a reduced space of variables.

Results

The sequence of Bagliettu is made up of three sedimentary units (Figure 2): algal-rich organic sediment with silts to coarse sands from 240 to 195 cm in depth, Cyperaceae peat from 195 cm to the top and, two interbedded layers of amorphous peat between 78–50 and 35–0 cm (the latter being rich in *Erica terminalis* roots). The seven calibrated ^{14}C dates and the age-depth model are presented in Figure 2 and Table 2. All ages are within the 2-sigma envelope of the age-depth model and are stratigraphically coherent. According to this model, the bottom of the profile is dated to 3940–3650 cal. BP (2σ interval). A hiatus of about 1800 years at 78 cm depth (Figure 2) is inferred from both the age-depth model and lithological changes. In total, 188 insect taxa were identified, including Coleoptera, Diptera, Heteroptera, Hymenoptera: Formicidae, Orthoptera Gryllotalpidae and Trichoptera. Coleoptera is dominant with 170 taxa, 70

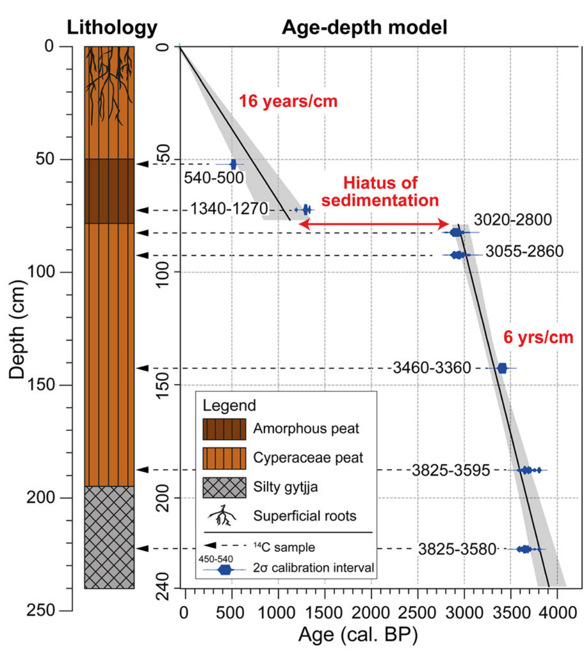

Figure 2. Lithology and age-depth model of the sedimentary profile of Bagliettu computed based on the probability density functions of the ^{14}C AMS ages. The bold line represents the best age-depth model solution and the grey envelope with the 95% confidence interval.

of them are identified at species or species-group level. Thirty-four plant taxa were identified. Five independent Insect Assemblage Zones (IAZ-1 to -5, Figure 3A) and Plant Assemblage Zones (PAZ-1 to -5, Figure 3B) were defined according to the depth-constrained cluster analysis. These independent zonations are approximately synchronous.

From 3920 to 3670 cal. BP (IAZ-1/PAZ-1), insect and plant richness are low (16 and 10 taxa respectively). The assemblages are composed of hygrophilous beetles with affinities for muddy riverbanks (*Limnichus, Dryops*) and sandy soils (*Scopaeus*), together with a few remains of wetland plants (*Carex* and *Lycopus europaeus*). The remains of *Alnus* and the xylophagous *Xyleborinus saxesenii* indicate the presence of woodlands. As the coring site is located in the floodplain of the Asco river, this period was probably characterised by high lateral river mobility, favouring a regular rejuvenation of the surficial sediments, which is not favourable to trap biotic fossils.

From 3670 to 3220 cal. BP (IAZ-2/PAZ-2): Insect abundance and richness were high (126 taxa), and so was plant diversity (21 taxa). An acidic peat-bog was developing at a rate of 16 y/cm, with high abundances of *Carex* (including *Carex echinata*), *Eupatorium cannabinum* and *Lycopus europaeus*. Some insect taxa similarly provide information about the local flora: *Donacia marginata* eats leaves of *Sparganium* (Koch 1989–1992), some Phalacridae feed on smut spores infecting *Carex* (Thompson 1958). Besides peat-inferred taxa, high abundances of wetland-dependent insects, attesting both running and standing water conditions, are represented by Trichoptera and various beetles (for example, *Agabus bipustulatus, Hydroporus memnonius, Rhithrodytes sexguttatus, Hydraena testacea, Limnoxenus niger*). Wood/tree-dependent polyphagous Coleoptera species associated with broad-leaved trees (for example, *Choerorhinus squalidus, Stenoscelis submuricata, Xyleborinus saxesenii, Melasis buprestoides*), stenophagous species mainly found on *Quercus* (*Salpingus planirostris, Platypus cylindrus*) and rosaceous fruit trees (*Magdalis cerasi, Scolytus rugulosus*) cohabited with insects of more open wet habitats, such as *Cercyon rhomboidalis* (a Corsican endemic species), *Limnichus* and *Scopaeus*. This picture of a diversity of habitats and patchy vegetation is supported by abundant *Alnus* remains, and the underlying presence of *Rubus, Sambucus* and *Vitis vinifera*. Finally, Coleoptera associated with disturbed grounds (arable soils with the presence of mammals) such as *Diplapion confluens* (feeding on *Matricaria* and *Anthemis*) and *Protapion* (mainly feeding on *Trifolium*) is also abundant.

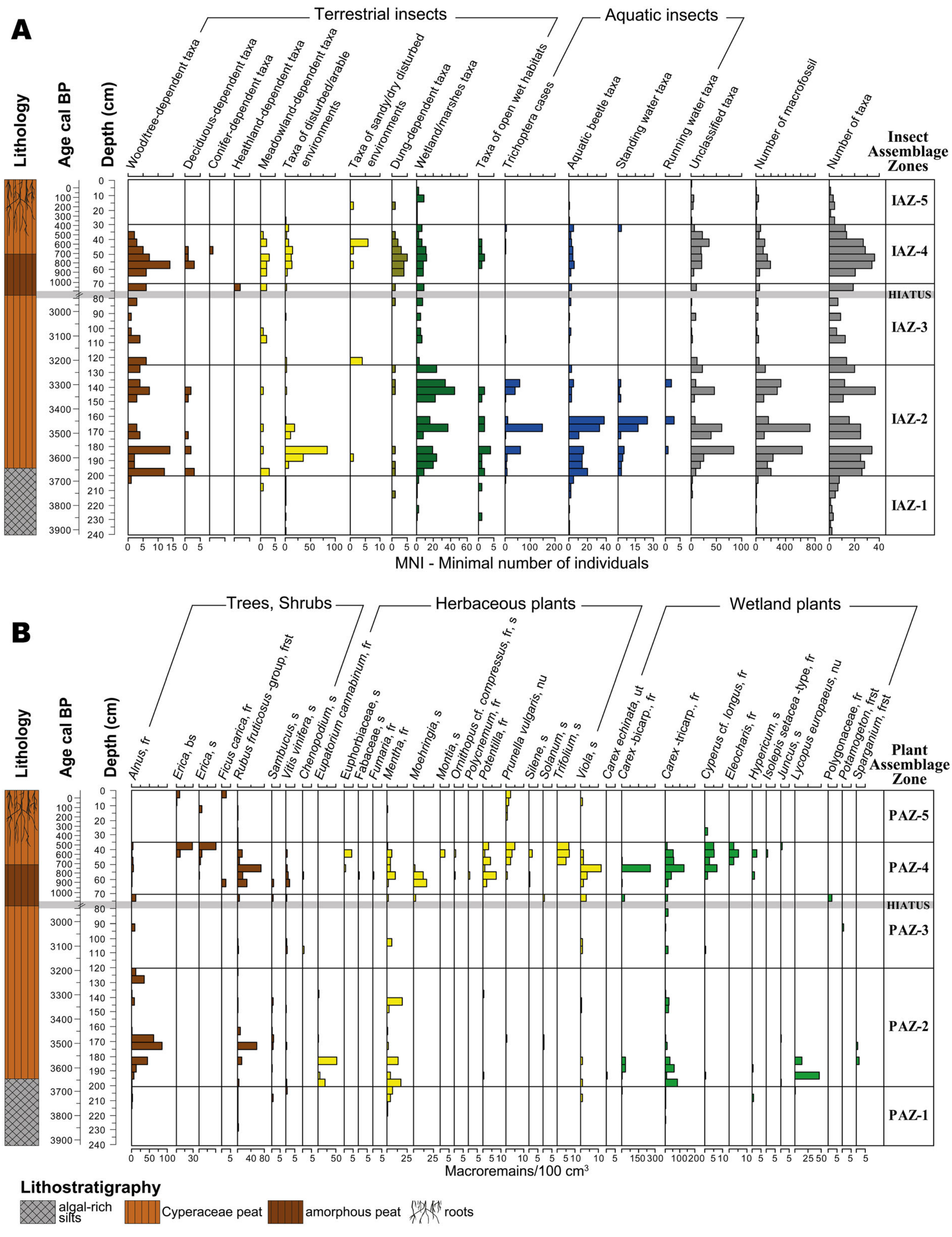

Figure 3. Fossil remains identified in the sediments of the wetland of Bagliettu represented according to the core depth (cm) and the corresponding best-modelled age (years calibrated Before Present). The horizontal grey band symbolizes a sedimentary hiatus. **A** Simplified entomological diagram expressed as Minimum Number of Individuals (MNI) per sample. IAZ: Insect Assemblage Zone. **B** Plant macrofossils diagram expressed in concentration (number of macro remains per 100 cm^3). *Fr* fruit, *s* seed, *bs* buds, *frst* fruitstone, *nu* nutlets, *ut* utricle. PAZ plant assemblage zone.

From 3220 to 1020 cal. BP (IAZ-3/PAZ-3): 61 insect taxa and 15 plants were identified. Insects associated with wetland/marshes decrease and those from open, wet habitats and standing water almost disappeared. Hygrophyte plant taxa are represented by few remains of *Carex*, *Cyperus longus* and *Potamogeton*. The diversity of wood/tree-dependent insects remains relatively stable, accounting for 30% of the terrestrial fauna. Some new insect taxa, such as *Agelastica alni* feeding on alder leaves, and *Hemicoelus* cf. *fulvicornis*, a wood-borer insect associated with broad-leaved trees, are recorded. In general, the persistence of all the ecological groups of insects while assemblages become impoverished suggests that no drastic environmental changes took place at that time, but more probably a decrease of the overall level of humidity, possibly associated with phases of oxidation, as is suggested by the hiatus at the end of IAZ-3.

From 1020 to 390 cal. BP (IAZ-4/PAZ-4): This period shows the most diversified assemblages (100 insect taxa, 29 plant taxa) with insect communities associated with meadows (*Chaetocnema arenacea*, *Chrysolina* cf. *viridana*, *Diplapion confluens*, *Protapion* and *Gymnetron*), the abundance of phytophagous leaf-beetles and weevils that feed on herbaceous plants. Plant assemblages are characterized by Euphorbiaceae, Fabaceae, *Fumaria*, *Montia*, *Ornithopus* cf. *compressus*, *Polycnemum*, *Silene* and *Trifolium*, *Hypericum*, *Moehringia*, *Potentilla*, *Prunella vulgaris* and *Viola*. The development of grasslands is associated with peat growth (Cyperaceae, with *Carex*, *Cyperus* cf. *longus*, *Eleocharis*, *Isolepis setacea*-type) at a rate of 16 years/cm. Coprophagous beetles (for example, *Bubas bison*, *Caccobius schreberi*, *Onthophagus ruficapillus* and *Sisyphus schaefferi*) are abundant, which suggests the presence of mammals on the peat-bog. The vegetation was probably open but broadleaved-tree stands were also present, as suggested by the arboreal ant *Dolichoderus quadripunctatus* (Torossian 1968), various phytophagous/xylophagous beetles (for example, *Curculio*, *Platypus cylindrus*, *Scolytus rugulosus* and *Trixagus dermestoides*), the riparian-dependent beetles *Agelastica alni* and *Stenoscelis submuricata* as well as the weevil *Micrelus* cf. *ferrugatus* that indicates the presence of heather [25].

From 390 cal. BP to Present (IAZ-5/PAZ-5): The insect assemblages are poor (13 taxa) and corroded. Plant assemblages are also poor (9 taxa), reflecting the presence of *Erica* stands and understorey vegetation characterised by *Prunella vulgaris* and *Viola*. The expansion of *Erica terminalis* together with the drying up of the peat-bog did not provide appropriate conditions for peat growth nor fossil preservation. Dung-beetles (*Aphodius*) and grassland weevils (*Protapion*) coexist with some remaining water or riparian beetles (*Contacyphon*, *Carpelimus*, *Dryops* and *Hydroporus*) suggesting that landscapes were similar to today, dominated by pasture grounds with scarce open woodlands and scattered water bodies.

Discussion

A Two-Phase Successional Pathway

The results provide insights into the original ecological trajectory of the Bagliettu peat-bog over the last 3900 years. The site has recorded two ecological successions during its life span (Figure 4): a first succession from 3900 to 3000 cal. BP, followed by an absence of fossil record of two millennia and, a second succession from 1200 cal. BP to Present.

These two ecological successions show some similarities. First, the successions start with an environmental baseline marked by no or little sediment deposition and low insect preservation (that is, a newly abandoned riverbank and a paludification phase (see the white dots in Figure 4). After a couple of centuries, environmental conditions progressively changed to waterlogged vegetation allowing organic matter preservation and sedge peat growth (phase 1, Figure 4), in association with abundant and diversified insect assemblages (phase 2, Figure 4). This relatively stable situation of rich and diverse habitats lasts for three to five centuries and then shifts toward an unstable phase with the persistence of the former ecological groups, but taxonomically poorer (phase 3, Figure 4). Such regressive dynamics may be compared to general models proposed for boreal-temperate regions (for example, Rydin and Jeglum 2013) describing the evolution of peat bogs with (1) starting processes of paludification in minerogenic and vegetation-free contexts, (2) followed by first peat formation with an initial increase in species diversity and richness that generally evolves with time to closed ligneous vegetation installation, and (3) to a drying-up, which is associated with poorer ecological assemblages. Therefore, such dynamics, which may be summarized by the simplistic opposition between ''wetter-richer'' (wetter peat, richer species diversity) and drier-poorer may be appropriate, at first, for characterizing the four millennia-long ecological evolution of the wetland.

However, if the progressive successional trends of Bagliettu present some similarities, it is worth noting that the most diverse insect and plant assemblages of these two periods (the two phases

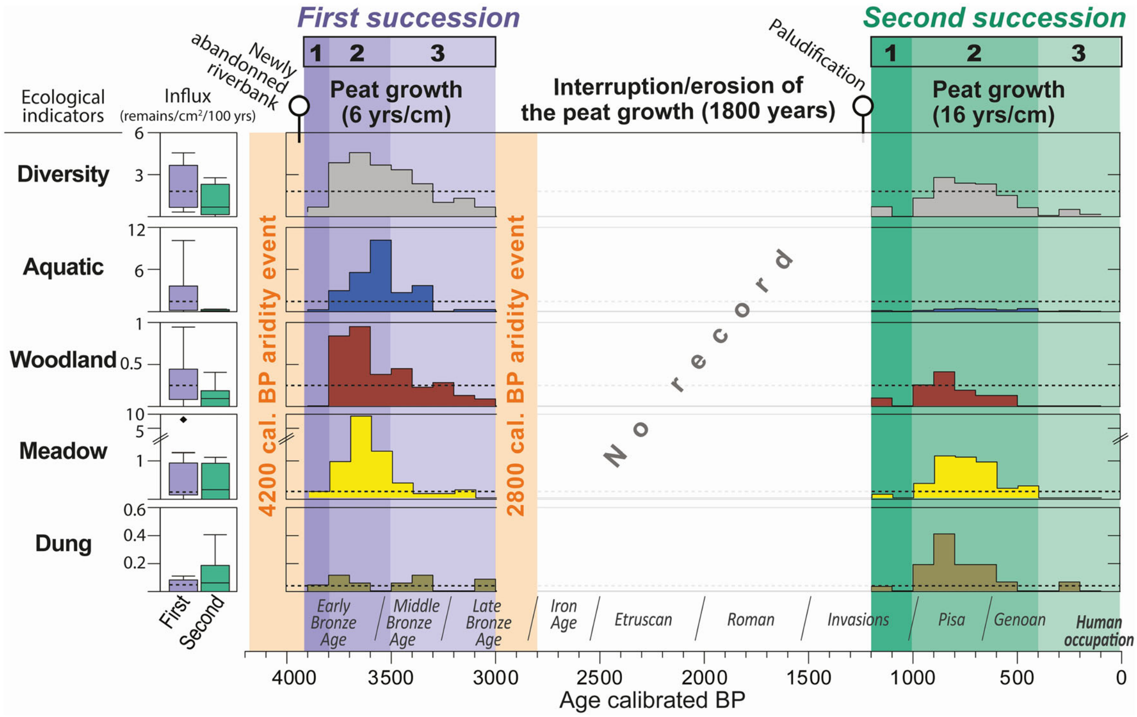

Figure 4. Long-term ecological successions of the Mediterranean wetland of Bagliettu evidenced by a selection of meaningful insect-inferred indicators influxes (that is, diversity, aquatic, woodland, meadow, dung) that are represented by step-curves according to a constant time-interval of 100 years. Three phases of ecological successions (phase 1: waterlogging and early stage of organic deposition, phase 2: abundant and diversified insect assemblages; phase 3: persistence of the former groups, but poorer) are highlighted in a gradient of purple (first succession) and green bands (second succession), interrupted by a recessional phase (hiatus or erosion) represented in light grey. The boxplots sum up the individual distributions of the two successions. The dashed line displays the median influx values of the first succession. Two regionally recognized climate aridity event are shown in orange. An indicative chronology of the human occupation and rulership of Corsica is shown.

n°2, Figure 4) reflect different vegetation covers. From 3900 to 3000 cal. BP, the peat-bog was growing at a rapid rate (6 years/cm), characterized by a high abundance of aquatic and wetland species, and was covered by woodlands of denser canopy cover, with open patches. This situation significantly contrasts (see the boxplots in Figure 4) the period 1200–400 cal. BP, where peat growth rate was 3 times slower and the vegetation dominated was by a meadow with few stands of broadleaved trees (a drop to low woodland values while meadow remained at the same values, Figure 4), and showing significant signs of mammal disturbances. These interpretations are reinforced by the results of the Principal Component Analysis (Figure 5A) that likewise display two distinct successional pathways, characterised by a first ecological succession (purple arrow in Figure 5A), ending with an interruption/erosion of the peat growth for a period of 1800 years, similar to the initial baseline, and followed by a second succession that is today in its impoverished phase (green arrow in Figure 5A). This long interruption of peat formation reflects a drastic change in the local environmental factors which constrained the second ecological succession.

Driver of Tipping Points in the Ecological Functioning

Geomorphic Evolution

Changes in the hydrological budget, geomorphic features, or superficial erosion are typical factors shaping the ecological characteristics and richness in peat-bog successions (Rydin and Jeglum 2013). At Bagliettu, the persistence of water saturation of the peat over the year is one critical point: the drop to lower values of aquatic-inferred insects (Figure 4), tallies concomitantly with a slowdown of the peat growth rate (6–16 year/cm), suggesting that the water budget was proportionally higher during the first succession than during the second. For comparison, high latitude boreal regions are characterised by rates of about 100 y/cm (Martini

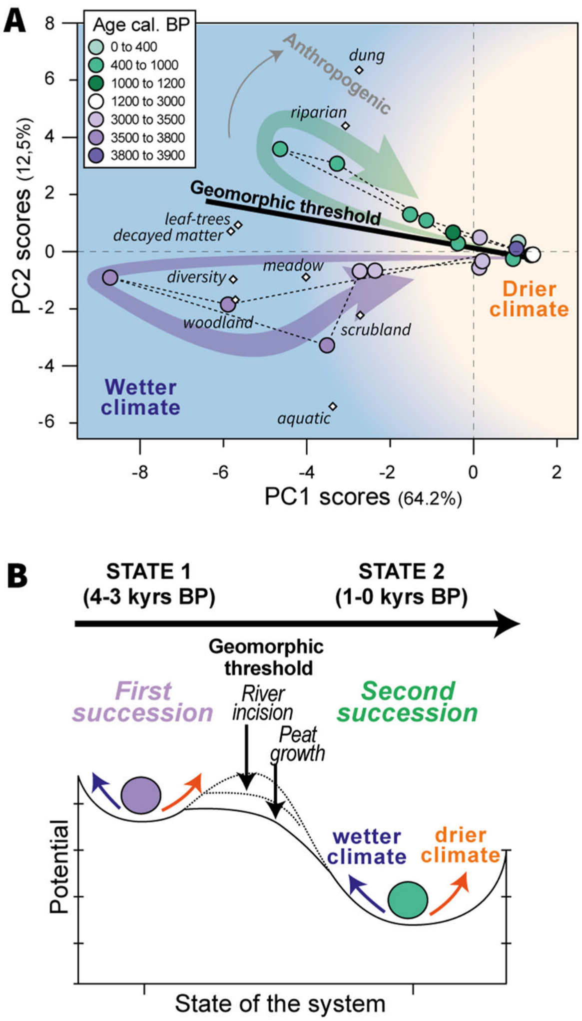

Figure 5. Interpretation of the millennial-long ecological functioning of the Mediterranean wetland of Bagliettu. **A** Principal Component Analysis (Components 1 and 2) carried out on the homogenized dataset of 39 individuals representing 100 years interval each [circles], and 9 ecologically meaningful variables [diamonds]. The individuals are grouped by phases of successional stage (gradients of purple and green). The dashed lines connect the individuals according to time. A visual guide of interpretation includes the two succession pathways of the peat-bogs (purple and green thick arrows) during relatively wetter climate (blue area), going back to a similar null position in the oriented space, that has been synchronic with drier climate (orange area). A rotation of the individuals toward drier peat conditions is interpreted by the occurrence of the geomorphic threshold (thick black line). Propensity of higher anthropogenic disturbances in the recent time suggests the potential occurrence of a second ecological threshold (light grey). **B** Schematic representation of the geomorphic-induced regime shift that, by amplifying impacts of climate aridification, has precipitated, 3000 years ago, the wetland ecological functioning to a new, different regime of variability.

and others 2006), whereas temperate regions (for example, central European) have rates similar to the modern ones reconstructed at Bagliettu (15–25 year/cm). The highest rates are observed in tropical regions, where saturation in humidity is associated with warmer temperatures (for example, 2 year/cm in Borneo). More contrasted situations exist in the Mediterranean, depending on the duration of summer droughts and precipitation regimes. For example, Holocene peat accumulation rates stood at about 9 year/cm in the southern France (Triat-Laval and Reille 1981), similar to the Spanish littoral (Brisset and others 2020). Our results argue that, if the humidity conditions are low but persistent over the year, peat can grow at quite rapid rates in the sub-humid dry Mediterranean region.

From a hydrogeomorphic point of view, lower humidity conditions are likely explained by the long-term vertical incision of the river, leading to the modern situation of the peat-bog perched at 1.5 m above the active channel. This incision trend is observed in Corsica (Hewitt 2002) as well as in other Mediterranean regions (Brisset and others 2014). The disconnection of the alluvial nappe has undoubtedly accentuated the vulnerability of the peat-bog to a shorter-term hydrological variability. A source of water recharge from the fractured bedrock has been identified at Bagliettu, but its contribution is not well-understood. Quantifications made for Valdu, another peat-bog of the same river valley, show that this source is minor compared to the Asco River one, but it maintains the water table high enough to keep the peat-bog fed during the driest months (Santoni and others 2021). It can be therefore assumed that lateral water sources are likely to have compensated humidity losses triggered by the river incision (Figures 4 and 5B), allowing a paludification of the site 1200 years ago, after 1800 years of interruption.

Climate Changes

In addition to geomorphological forcing, this successional pathway might have been influenced by shorter-term stressors of the hydrological balance which trigger peat development and interruption (Figures 4, 5A). In palaeoclimatological records from the Western Mediterranean, a series of centennial-scale aridity events were recognized (Frigola and others 2007), corresponding to North Atlantic oscillations (Bond and others 2001), among them, one at about 4200 cal. BP and the other at 2800 cal. BP (symbolized by yellow bands in Figure 4). The 4200 years BP climate event was identified as an arid phase in the Southern Alps (Cartier and others 2019), the Apennine (Drysdale and others 2006) and Algeria (Ruan and others 2016) whereas the 2800 cal. BP climate event already occurred in a long aridity phase between 3000 and 2000 cal. BP. In some sites tied to water springs activation (Carrión and others 2001; Brisset and others 2020), this event is also marked by a local drying up. The contemporaneity of aridity events with interruption of the peat-bog evolution of Bagliettu (Figure 4) therefore suggests that climate changes have been a major factor modulating peat-bog humidity (Figures 4B, 5A), and thus ecological functioning. The re-activation of the peat formation at about 850–1350 cal. BP (2σ age interval) corresponds to wetter climatic conditions acquired at about 1700 cal. BP in the Western Mediterranean (Cartier and others 2022), promoting amorphous peat formation and higher insect diversity during the period of rainfall maxima of the Little Ice Age (Oliva and others 2018; Cartier and others 2022).

Anthropogenic Disturbances

Occurrences of insects associated with dung and arable lands appear from the beginning of the record (that is, 4000 years ago), which raises the question of ancient human impact. The history of the peopling of the island begins about 7400 years ago (Revelles and others 2019): therefore, the hypothesis of pastoral activities during the first peat-bog succession is likely. The insect assemblages suggest that disturbances associated with mammals trampling were, however, much higher during the second peat-bog succession than during the first one (Figures 4, 5A). In the vicinity of Bagliettu, the Castrum of Rostino (twelfth-fourteenth centuries) provides evidence of intensive caprine farming (Cucchi 2003). This period corresponds to the Genoan occupation of Corsica (Figure 4), marked by intense agropastoral activities (Vigne and Valladas 1996), forest clearance, and fire at higher altitudes (Leys and others 2014). The Roman and Medieval periods are not covered by the Bagliettu record but there is no doubt that human activities also played a role in shaping landscapes at that time (Reille 1992).

Inherited and Ongoing Trends

The peat bog persisted for about 800 years, and then returned as a different type of wetland 1800 years later, and this later wetland persisted from 1200 cal. BP until the present, showing a relative plasticity to hydro-climate changes. In contrast, the recent history reveals that the ecosystem became particularly sensitive to disturbances (Figure 5A). The 1800-years sedimentary hiatus specifically points out that, once the geomorphic threshold was crossed due to the river incision, arid climate events deeply affected the ecosystems (Figure 5B). In other words, the ecosystem developed a major dependence on superficial water inputs, that also became less abundant. Superimposed on this long-term forcing, an arid pulse triggered the demise of an accumulating wetland. A ''new'' state (state 2 in Figure 5B) developed some 1800 years later. This highlights that past period of drought had severe consequences on the ecosystem trajectory and thus may be considered as a prefiguration of future changes that will occur in the light of projections of aridification of the Mediterranean climate (MedECC 2020). With the added effects of anthropogenic disturbance, which has been identified as increasing in the fossil record, these conditions might lead to the disappearance of the wetland.

Insight on Conservation

This type of peat-bog within the Mediterranean bioclimate is very rare and deserve protection. Bagliettu peat-bog includes several priority habitats included in the European Directive (92/43/EEC), and some plant associations characterizing temporarily flooded wet grasslands (*Baldellio ranunculoidis-Lythretum salicariae, Platanthero algeriensis-Juncetum effusi*) are only known from this site (Gamisans and others 1998). Several remarkable plant species listed in Table 1 (Gamisans and others 1998), and one semi-aquatic Coleoptera (*Cercyon rhomboidalis*) being endemic to Corsica and Sardinia, were reported. These species are rare to very rare in Corsica, which justifies strict conservation actions.

Nevertheless, rural abandonment, initiated in the mid-nineteenth century, and the lowering of the water table is leading to a re-colonization of the bog by alders, pines and heather (Gamisans and others 1998; Delbosc and others 2015). Extensive grazing and forest management have been thus recommended to tackle a closing and drying out of the wetland. However, as visible in the site, cattle roaming freely alters the peat bogs by trampling, inducing the formation of deep wet gullies that increase the drainage, lower the water table, and thus promote erosion. Although grazing helps to maintain the wetland open and specifically favours the survival of heliophilous taxa, management by grazing will not protect the ecological functions.

Other consequences of reintroducing grazers may be the local extinction of remarkable species, including endemics. However, because *Drosera rotundifolia* is not a native plant at Bagliettu, and *Liparis loeselii* has not been recorded since 1996 (Conservatoire Botanique National de Corse, pers. com.), the relevance of maintaining the ecosystem in its current state is questionable. The other peat-bog of the river valley (Valdu), being the largest active ombrotrophic bog with *Sphagnum* in Corsica, is probably a more valuable target for conservation. A closer position to the aquifer makes this wetland comparable to a young stage of the geomorphic evolution of Bagliettu, and thus probably more suitable for long-term conservation actions.

Conclusion

Historical Ecology applied to a Mediterranean wetland revealed that this peat-bog has thrived several millennia with a relative resilience to short-term perturbations. However, reduced wetland connection due to river incision play a major role in the long-term degradation of wetlands, unlikely reversible at our human scale. Superimposed on this long-term geomorphic threshold, aridity events are important pulses to trigger a shifting of the ecosystem to a new, different state. These results have major implications for our understanding of ecological functioning when subjected to both long-term and short-term perturbations, that can lead to regime shifts. ''Past'' case studies can actually be considered as providers of empirical data prefigurating realistic future ecosystem changes, in the light of the climatic projections. So, even if reclamation actions are initiated on such a site, this case study suggests that ecosystem losses might occur independently of change in precipitation regime, because of now being deeply impacted by human activities. Not being partisan of *laissez-faire*, it argues that understanding long-term successional trends systematically must be considered before engaging conservation efforts.

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