The application gap: genomics for biodiversity and ecosystem service management

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47 Highlights

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- Genomic knowledge can benefit biodiversity and ecosystem services (ES) management
 - Genomics benefits are underachieved: there is an application gap in ES management
 - We propose a framework for genomics-informed biodiversity and ES management actions
 - Actions tackle conservation, adaptation, productivity, invasives, restoration
 - Policy developments and scientists-managers synergies are needed to bridge the gap
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55 Keywords

- 56 Genomics, sustainable ecosystem services, biodiversity conservation, management goals,
- 57 management actions, evolutionary processes
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- 59

60 Abstract

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62 The conservation of biodiversity from the genetic to the community levels is fundamental for the 63 continual provision of ecosystem services (ES), the benefits that ecosystems provide to people. 64 Genetic and genomic diversity enhance the resilience of populations and communities that underpin 65 the provision of ecosystem functions and services. We show that genomics applications are mostly 66 limited to flagship species and that their benefits for biodiversity conservation and ES management 67 are underachieved. We propose a framework on how genomics applications can guide management 68 for biodiversity conservation and sustainable ES to bridge this genomics-ES management 'application 69 gap'. We review how genomic knowledge in single species (relatedness, potentially adaptive variants) 70 or in interacting species (host-microorganism coevolution, hybridization) can guide effective 71 management actions. These include population supplementation, assisted migration or hybridization 72 to promote climate-adapted variants or adaptive potential, control of invasives, delimitation of 73 conservation or management areas, provenancing strategies for restoration, managing microbial 74 function and solving conservation and ES trade-offs. Genomics-informed management actions for 75 improved conservation and ES outcomes are supported through synergies between scientists and ES 76 managers at local, regional and international levels, through the development of standardized genomic 77 workflows, training to ES managers and incorporation of local information. Such actions facilitate the 78 implementation of biodiversity conservation and ES policies such as the UN 2030 sustainable 79 development goals and the EU Biodiversity strategy for 2030, and support the inclusion of ambitious 80 biodiversity conservation goals in the development of new policies such as the CBD post-2020 Global 81 Biodiversity Framework or conservation policies on hybrids.

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83 A. Introduction

84 Managers of terrestrial or aquatic ecosystems increasingly use scientific evidence to design strategies 85 for biodiversity conservation, its sustainable use and the sustainable provision of ecosystem services (Addison et al., 2017; Bland et al., 2017; Keith et al., 2013; Milner-Gulland and Rowcliffe, 2007; 86 87 Perrings et al., 2011). Ecosystem services (ES) are the benefits that ecosystems provide to people 88 (Haines-Young and Potschin, 2018). Sustainable ES and human well-being critically rely on 89 biodiversity, which encompasses the diversity of ecosystems, species, and genes (Bennett et al., 90 2015; Díaz et al., 2018; Reid et al., 2005). Biodiversity drives ES through sustaining ecosystem 91 functions and enabling the resilience of populations, species and communities (Breed et al., 2019; 92 Mace et al., 2012; Stange et al., 2021). As global assessments document alarming rates of 93 degradation of biodiversity, ES and the climate (CBD, 2020; Fao and Unep, 2020; IPBES, 2019; IPCC, 94 2020; WWF, 2020), there is an increasing urgency and necessity to preserve and restore life-95 sustaining biodiversity for ES management (Breed et al., 2019; Keith et al., 2013; Mace et al., 2012; 96 Oliver et al., 2015; Stange et al., 2021).

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98 Ecosystem managers have given different levels of attention to biodiversity among and within species.

99 The diversity of species, their functions and interactions are regularly considered (Barbaro et al., 2017; Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service management. *Biological Conservation* 2023 ;Volum 278. <u>10.1016/j.biocon.2022.109883</u> CC-BY-NC-ND

100 Brockerhoff et al., 2017: Cadotte et al., 2011: Dee et al., 2019: Lavorel et al., 2013), but the underlying 101 genetic diversity within species is less conspicuous and remains often overlooked (Hoban et al., 102 2021b; Laikre et al., 2020, 2010). Genomic diversity, i.e. genetic diversity at the genome-wide level, is 103 composed of DNA variants that are mostly neutral to natural selection, and of variants that can respond 104 to selection, affecting individual fitness and population adaptation. Genomic diversity is responsible 105 for the level of adaptation of populations to their current environment, and for their adaptive potential 106 (Derry et al., 2019; Hoffmann et al., 2017) which enables them to adapt to environmental change and 107 increases their resilience to anthropogenic risks (Hoffmann and Sgrò, 2011; Hughes and Stachowicz, 108 2004; Sgrò et al., 2011; Wernberg et al., 2018). The natural resource manager can harness this 109 genetic diversity information for an evolutionary management of populations, with relatively fast 110 effects, in just one or a few generations, e.g., slowing down genetic erosion or producing a shift in 111 adaptive allele frequencies (Hairston et al., 2005; Rudman et al., 2017). Recent reviews have 112 highlighted the relevance and application potential of genomics for biodiversity, ecosystems and 113 people (Breed et al., 2019; Stange et al., 2021). However, despite available scientific knowledge, 114 methods and guidance, the integration of genetic and genomic information into international policy on 115 biodiversity conservation and sustainable management is progressing slowly (Arlettaz et al., 2010; 116 Dubois et al., 2020; Shafer et al., 2015), notably with regard to the post-2020 global biodiversity 117 framework of the Convention on Biological Diversity (Hoban et al., 2021a,b; Laikre et al., 2020) and 118 the 2030 UN sustainable development goals (Huddart et al., 2022; Mondejar et al., 2021).

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120 In this paper we focus on genomic variation and its applications to facilitate biodiversity conservation 121 and management for the sustainable provision of ES. Using a literature keyword search and the review 122 of papers relating to specific ES management goals, we illustrate how genomic applications appear to 123 have poor representation in the ES literature and how their use is still largely focused on a few flagship 124 species. Consequently, benefits from genomics are underachieved, a reality we can qualify as a 125 genomics-management 'application gap' (see also (Taylor et al., 2017)). We illustrate solutions to 126 bridge this gap which extends beyond the earlier defined conservation genetics gap and its proposed 127 solutions (Hoban et al., 2013a; Holderegger et al., 2019). We show how genomic data captures 128 relevant conservation and management information in single and in interacting species (e.g., inbreeding, population structure, adaptive genetic variation, symbiotic interactions, co-evolutionary 129 130 history) and how this information is actually or potentially used to support management actions to 131 effectively attain ES-related management goals in a broad range of ecosystems.

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133 Our paper comprises four sections: 1) A section on the concepts and our proposed framework relevant 134 to genomic applications in natural and weakly to moderately managed ecosystems; 2) a Methods 135 section that describes our approach of reviewing the literature; 3) a core section that addresses the 136 application gap and illustrates with case studies how genomics can facilitate conserving biodiversity 137 and achieving a large range of species-level and community-level management goals for ES; and 4) 138 a Discussion section that summarises our findings on genomics for biodiversity conservation and ES 139 management and discusses their implications for improved research and biodiversity management in 140 an international conservation context.

B. Concepts and framework for sustainable genomics-informed biodiversity conservation and ecosystem service management

143 B1. Ecosystem services and a suggested framework for their sustainable management

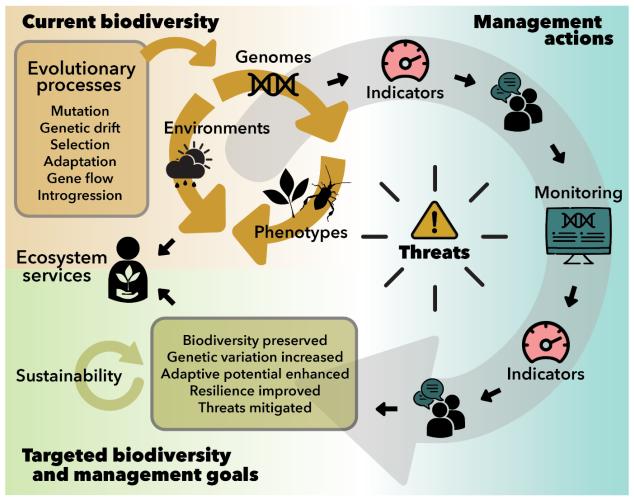
144 Ecosystem services are defined by the Common International Classification of Ecosystem Services 145 (CICES, supported by the European Environmental Agency) as the contributions that ecosystems 146 make to human well-being, and are considered to be distinct from the goods and benefits that people 147 subsequently derive from ES (Haines-Young and Potschin, 2018). The CICES v. 5.1 framework 148 defines three ES Sections: Provisioning ES, Regulation and maintenance ES, and Cultural ES. The 149 concept of ES was popularised in the Millennium Ecosystem Assessment (Reid et al., 2005) and was 150 further developed into the concept of 'Nature's Contributions to People' (NCP) by the 151 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) to 152 explicitly recognize the role of culture and local knowledge in shaping the relationship between nature 153 and people (Díaz et al., 2018); for correspondence between the ES and NCP frameworks, see 154 Kadykalo et al. (2019). Since specific ES are relatively straightforward to identify from an ES 155 management point of view, and since they are commonly linked to a particular species or function 156 within an ecosystem, we mainly use the ES concept in this paper.

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158 We propose a conceptual framework for effective and sustainable genomics-informed biodiversity 159 conservation and management of ES as detailed in Fig.1. The ecosystem manager first has to define 160 a management goal that aims to maximise one or multiple ES (Villarreal-Rosas et al., 2020), while 161 also preserving the ecosystem with a high level of biodiversity for future needs under uncertainty (Grêt-162 Regamey et al., 2013; Hamel and Bryant, 2017). To establish a management plan, they must identify 163 ecosystem biodiversity reference points in time, such as i) the current biodiversity in the ecosystem 164 before management actions are applied, and ii) the biodiversity at a specific future time point in which the targeted management goal will be achieved (Fig. 1). Indicators based on species diversity. 165 166 genomic, phenotypic and environmental diversity can be used to measure the biodiversity status and 167 eco-evolutionary processes of the ecosystem and the ES it provides. This is useful to understand and 168 predict effects of potential threats to biodiversity and the ES (Keith et al., 2013), to provide insights 169 into the mitigation of these threats, and thus to contribute to designing management actions to achieve 170 the management goal (Fig. 1). Monitoring the change in these ecological and evolutionary indicators 171 and adjusting management action as necessary is key for successful biodiversity conservation and 172 sustainable ES management (Hoban et al., 2020). Collaboration between managers and scientists is 173 highly relevant in this process, to exchange information, samples and methods.

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176 Figure 1 Framework to reduce the application gap of genomics in biodiversity conservation 177 and ecosystem service management. Current biodiversity and ecosystem services (ES) are 178 affected by evolutionary processes that modulate genomic diversity. Managers can use indicators 179 based on genomic, phenotypic and environmental diversity to assess and understand this current state 180 of an ecosystem and to inform which management actions lead to the targeted management goals. 181 Collaboration between managers and scientists is highly relevant in this process, to exchange 182 information, samples and methods. Threats can affect all stages of the ecosystem and its 183 management, but monitoring and adjustment of management actions will make it possible to achieve 184 the management goals in which the targeted biodiversity can sustainably provide ecosystem services. 185 The colour codes used are the same in figs. 1, 2 and 3, i.e. orange for genomic and other data, blue 186 for management actions and green for management goals.

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188 **B2.** Evolutionary processes and the added value of genomics for biodiversity 189 conservation and ES management

Different evolutionary processes affect biodiversity and thus ES provision: speciation and hybridization
events shape species diversity, and mutation, genetic drift, gene flow and selection shape the genetic
diversity within species (Fig. 1), with potential effects on species interactions (Whitham et al., 2006).
Both these levels of genetic or genomic diversity, within single species and in systems of interacting
species, are thus relevant for conservation and ES provision (Fig. 2, see also Methods).

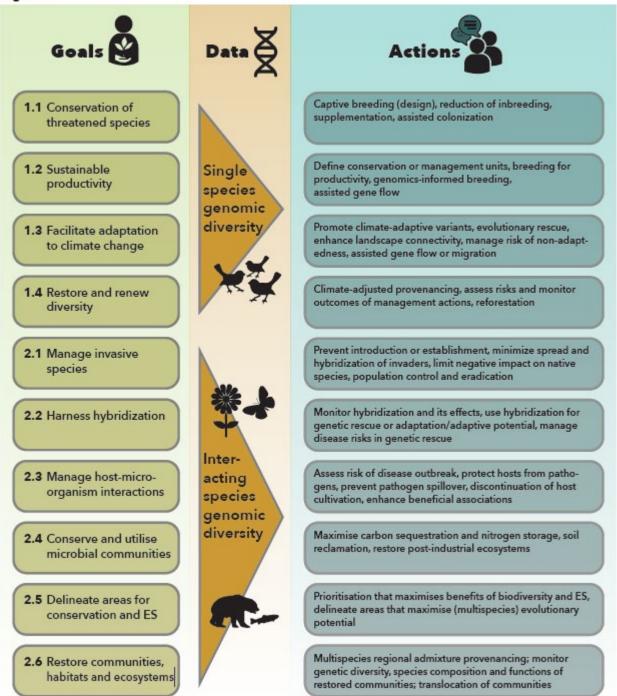
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196 High-throughput sequencing technologies have made it possible to study evolutionary processes at 197 the genomic level in model and in non-model organisms (Ekblom and Galindo, 2011; Formenti et al., 198 2022; Rajora, 2019). The main advance compared to previous technologies is a 100-10,000 fold 199 increase in the number of genetic markers assessed (e.g., single nucleotide polymorphisms, SNPs) 200 which allows for more accurate estimation of evolutionary parameters and removes biases due to 201 uneven genome sampling (Peterson et al., 2012). Intra-specific genomic data informs on the level of 202 population genetic diversity (e.g., the risk of loss of genetic diversity through genetic drift), on the 203 relatedness among individuals and substructure of populations, on their connectivity through gene 204 flow, and on past demographic history including events such as population genetic bottlenecks or 205 expansions (Gaut et al., 2018). In addition, the increased quantity and density of markers allow the 206 detection of genomic regions or genes potentially involved in adaptive genetic variation, for example, 207 based on molecular signatures of selection (Nielsen, 2005; Pritchard et al., 2010) or their association 208 with relevant phenotypes or putative environmental drivers of selection (Flood and Hancock, 2017; 209 Rellstab et al., 2015).

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211 The provision of sustainable ES depends on the persistence and continued performance of the species that provide the ES ('ES species'), which relies on the sustainability and adaptive evolution of 212 213 biodiversity at all levels, as well as the ecosystem's stability (Hairston et al., 2005). Keystone species 214 are species that exert very large effects on other associated species in a community (Paine, 1995). 215 Their adaptive potential is therefore particularly important to consider for management alongside that 216 of the co-occurring ES species. A cost-effective genomics-informed ES management requires the 217 identification of keystone and ES species and populations, and a suitable study design, sampling 218 strategy and choice of genomic markers to inform on evolutionary processes within species and, in 219 some cases, in communities of co-occurring and/or interacting species (Angeloni et al., 2012; Blasco-220 Costa et al., 2021; Flanagan et al., 2018; Hoban et al., 2013b; Schielzeth and Wolf, 2021; Whitham et 221 al., 2006).





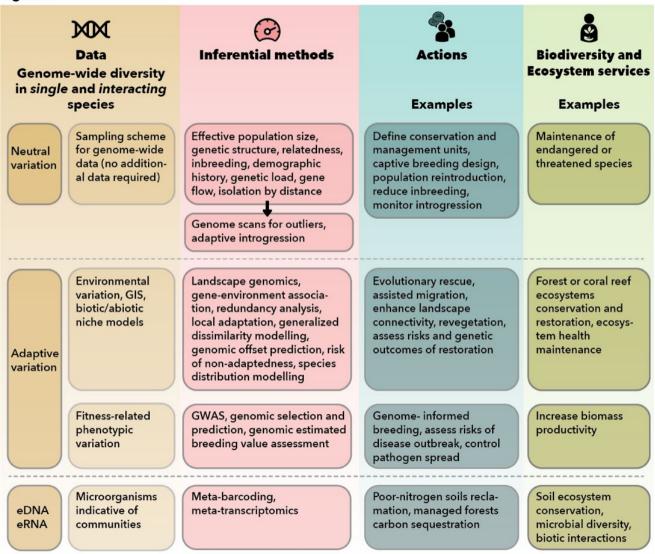
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Figure 2 The value of genomic diversity knowledge for biodiversity and ecosystem services 224 management goals and associated management actions. Management actions can be connected to 225 multiple management goals (see text).

226 C. Methods

227 To identify the best strategy to select the literature to review for this paper, we first evaluated the 228 potential of a systematic literature extraction. We conducted a terminology research on Pubmed 229 Central (www.ncbi.nlm.nih.gov/pmc/) to systematically and quantitatively examine the links between 230 the keywords 'genom' (contained in genome, genomic, genomics), 'biodiversity' and 'ecosystem 231 service' in the scientific literature. In over 6,000 papers that contained at least two of the keywords in 232 the full text, only nine mentioned 'genom' and 'ecosystem service' simultaneously in the abstract, 233 although both keywords co-occurred hundreds of times with 'biodiversity' (details in Supplementary 234 material S1). Studies on genomic applications that are relevant for ES management thus appear to 235 lack visibility in the scientific literature, or match poorly the terminology of ES (details on terminology 236 match with CICES V5.1 ES Sections and Classes in Supplementary material S1). The keyword search 237 suggested limited power for a systematic literature extraction; we thus defined our literature search in 238 consultation with natural resource managers. Based on our framework (Fig. 1), we developed a list of 239 management goals (MGs) in ecosystems that derive from natural biodiversity (Fig. 2). We selected 240 review papers and case studies pertaining to each MG, structured into the categories 'Single species genomic diversity' or 'Interacting species genomic diversity' to illustrate how management actions 241 242 (MAs, in **bold** in the text) for these MGs benefit from genomic data on a single species, or on multiple 243 interacting species (Fig. 2). We are conscious that some MGs are overlapping (Fig. 2) but list them 244 separately on purpose to enhance their accessibility to natural resource managers. When possible, 245 we preferred case studies that implemented genomics-informed MAs over those that only suggested 246 them. Given the wide scope of MGs, we did not aim to cover the literature on genomics and ES 247 management exhaustively. The main workflows that link genomic and other data to MAs are 248 summarised in Fig. 3.

Figure 3



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Figure 3 Methodological framework on how to use genome-wide diversity in association with phenotypic or environmental data to guide management actions for biodiversity and ecosystem services. The column "Data" is divided into types of genomic diversity data (left) and complementary data (right). GWAS, genome-wide association study; eDNA: environmental DNA; eRNA: environmental RNA.

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256 D. Genomic applications to support biodiversity and ES management

257 D1. Single species genomic diversity for biodiversity and ES management

258 Ecosystem managers have long recognized the importance of genetic diversity knowledge to define Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service management. *Biological Conservation* 2023 ;Volum 278. <u>10.1016/j.biocon.2022.109883</u> CC-BY-NC-ND

population boundaries and conservation units that maximise evolutionary potential and improve 259 260 population management (Funk et al., 2012; Moritz, 1994). Genome-wide data allow for powerful insights into neutral and adaptive evolutionary processes and their drivers in non-model species 261 (Ekblom and Galindo, 2011; Rajora, 2019). They promote the development of fast and effective 262 263 methods and MAs to mitigate the impacts of decreasing genetic diversity on populations, species 264 diversity, ES and climate change, as for example shown for the value of whales to sustain marine ES 265 (Attard et al., 2018; Cook et al., 2020). The main ES MGs that benefit from genomic data on single 266 species are listed in the following sections and include developing conservation strategies for 267 threatened species (D1.1), managing for sustainable productivity (D1.2), facilitating adaptation to 268 environmental change (D1.3), and restoring species in degraded ecosystems (D1.4).

269 D1.1 Conservation of threatened species

270 Conserving endangered species is a major MG that pursues the ES of preserving genetic resources 271 and products from rare species that can have significant functional roles in ecosystem processes (Dee 272 et al., 2019). It involves specific MGs on securing the persistence of populations and preventing 273 genetic erosion. MAs generally aim at increasing the number of individuals through supplementation. 274 for example from carefully **design**ed **captive breeding**, in order to **reduce inbreeding** and thus to 275 increase the diversity and adaptive potential of populations, or through assisted colonisation into 276 new habitats (Derry et al., 2019, Fig. 2, see also D2.2). Genomic applications that support these MAs 277 typically involve the estimation of relatedness, inbreeding, effective population size and, occasionally, 278 estimates of maladaptation or genomic load (Fig. 3, Arenas et al., 2021; Flesch et al., 2020; Leroy et 279 al., 2018). A recent workflow on how to use genomics to guide conservation MAs (Rossetto et al., 280 2021) rests on well-established paradigms in conservation genetics (Willi et al., 2022).

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282 One of these paradigms is that a severe reduction in population size is linked to reduced genetic 283 diversity (Frankham et al., 2014). For example, in the case of the hihi (Notiomystis cincta), a threatened 284 passerine bird endemic to New Zealand, a conservation programme starting in the 1980s used the 285 sole remaining island population as a source for reintroduction to the mainland and other islands but 286 failed to restore the species' adaptive potential (Brekke et al., 2011; de Villemereuil et al., 2019). Low 287 genome-wide diversity was correlated with low adaptive potential of individuals (estimated from long-288 term phenotypic trait and fitness data), which suggests genomic data can be used as a proxy for 289 difficult to obtain long-term trait data (de Villemereuil et al., 2019).

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291 Another case of severe population reduction is that of the Iberian lynx (Lynx pardinus), which declined 292 in the second half of the 20th century to only about 100 animals in two remaining subpopulations. A 293 captive breeding program successfully minimised inbreeding in ex situ conservation and in the 294 supplemented remnant populations (Kleinman-Ruiz et al., 2019). A new panel of 343 genome-wide 295 markers selected for minimal redundancy in the lynx genome (Abascal et al., 2016) demonstrated the 296 benefits of genomic markers, which outperformed microsatellites in four typical conservation 297 applications (individual identification, parentage assignment, relatedness estimation, and admixture 298 classification, Kleinman-Ruiz et al., 2017).

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300 While threatened plant species have been underrepresented in past sequencing efforts (Exposito-301 Alonso et al., 2020), a recent surge in the use of genomic data studies opens possibilities for more 302 efficient MAs in plant conservation (Lanes et al., 2018; Mamo et al., 2021; Tierney et al., 2020; van 303 der Merwe et al., 2021; Wagner et al., 2021). For example, *Ipomoea cavalcantei*, a narrowly distributed 304 endangered plant and a flagship species for tropical conservation, showed, unexpectedly, higher 305 genome-wide genetic diversity and lower spatial genetic structure than I. maurandioides, a widespread 306 species of least concern (Lanes et al., 2018). These results illustrate that genomic data are a useful 307 complement to the IUCN Red List Criterion B (extent of occurrence) in conservation assessments 308 (Garner et al., 2020).

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310 D1.2 Sustainable productivity

311 An important prerequisite for sustainable management of population productivity is the correct 312 delimitation of genetically distinct populations with different demographic or adaptive histories to 313 define conservation or management units (Fig. 2). For instance, genomic data is routinely used for 314 this purpose in sustainable fisheries management (Benestan, 2020; Bernatchez et al., 2017). The high 315 resolution of genomic data has made it possible to detect genetic structure in populations previously 316 assumed to be panmictic (Koot et al., 2021; Pazmiño et al., 2019), to provide information about the 317 directionality of gene flow between management areas (Barth et al., 2017), and to unveil mismatches 318 between administrative and biological units (Benestan, 2020; Mejía-Ruíz et al., 2020; Mullins et al., 319 2018). These genomic insights allow optimisation of management areas for productivity while limiting 320 the risk of overexploitation.

321 In many exploited species, the genomic underpinnings of biomass productivity traits (e.g., individual 322 growth), phenotypic plasticity and sensitivity to environmental stressors remain poorly known. In forest 323 trees, where genetic adaptation to the local population environment is common (Lind et al., 2018) 324 breeding programs for biomass productivity and disease resistance have traditionally been based 325 on phenotypic selection in pedigrees. SNPs associated with bud burst, drought resistance or wood 326 properties have been identified in some species (Gailing et al., 2009; González-Martínez et al., 2006), 327 but productivity-related traits are usually polygenic and may be shaped by negative selection (de 328 Miguel et al., 2022). Genomics-informed breeding, or genomic selection, takes advantage of this 329 polygenicity of traits allowing us to estimate the genomic estimated breeding value of each individual 330 based on genome-wide markers only, exploiting their associations with numerous small-effect 331 quantitative trait loci (Lebedev et al., 2020). In perennial species such as forest trees, genomic 332 selection allows for an early selection of individuals before trait expression and can outperform 333 pedigree-based selection while preserving genomic variation and adaptive potential (Pégard et al., 334 2020).

Assisted gene flow or migration to spread adaptive alleles is an option to boost productivity when allochthonous provenances outperform local ones, and is currently proposed to attenuate the impacts

of climate change (Aitken and Whitlock, 2013, see D1.3). The potential of this approach alongside genomic selection in a breeding program has been suggested for Norway spruce (*Picea abies*) in Sweden, where growth and phenology traits are polygenic and strongly geographically determined (Milesi et al., 2019). A study in lodgepole pine (*Pinus contorta*) showed that alleles associated with climate variables can be used to predict tree heights in a long-term provenance trial, illustrating the potential of genomic data to inform management if phenotypic trials are not available (Mahony et al., 2020).

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345 **D1.3 Facilitate adaptation to climate change**

346 Climate change affects all levels of biological organisation, changing species' distributions, species 347 interactions and population allele frequencies (Scheffers et al., 2016), which affects many ES of the 348 Provisioning and of the Regulation and Maintenance Sections. Climate change effects on ES are mostly negative although variable across services (Bindoff et al., 2019; Pecl et al., 2017; Runting et 349 350 al., 2017). Populations can respond to climate change by migration to track their climate optimum, 351 persist locally thanks to phenotypic plasticity or genetic adaptation, or face demographic decline and 352 increased extinction risk, the latter being exacerbated by loss of habitats (Aitken et al., 2008). 353 Predicting species and population responses to climate change is key to inform MA for their 354 persistence, especially if they lose suitable habitat or cannot track climate change through migration (Urban et al., 2016). These predictions have been improved with the inclusion of genetic structure 355 356 information into species distribution models (Ikeda et al., 2017), and the identification of climate-357 adaptive genetic variants through landscape genomics approaches (Capblancq et al., 2020; Razgour 358 et al., 2019: Rochat et al., 2021).

359 In European beech (Fagus sylvatica), a keystone species in temperate forests, genomic variants 360 associated with extreme phenotypes for drought damage were identified in natural panmictic 361 populations using a cost-efficient genome-wide association study (GWAS) on sample pools and then 362 validated in a genotyping assay that effectively predicted damage phenotypes (Pfenninger et al., 363 2021). These results can inform future MAs to facilitate adaptation to climate change in these forests. 364 In the bat species Myotis crypticus and M. escalerai, gene-environment association (GEA) methods 365 identified over 30 potentially climate-adaptive variants (Fig. 3, Razgour et al., 2019). Ecological niche 366 models that included these variants significantly reduced the geographic range loss predictions under 367 future climate scenarios, and can inform MAs for evolutionary rescue of threatened cold-wet adapted 368 populations through enhancing landscape connectivity and gene flow from hot-dry adapted ones 369 (Razgour et al., 2019).

Another approach to assessing climate change response is the prediction of genomic offset, or **risk of non-adaptedness** (RONA), i.e., the estimated level of maladaptation of a population to new environmental conditions based on genomic and environmental data from different time points and/or locations (Rellstab et al., 2021). For instance, current and future RONA estimates of *Betula nana*, a keystone woody species of conservation concern in Britain (Borrell et al., 2020) identify priority areas

375 for the conservation of local adaptations and adaptive diversity (see also D2.5) and propose assisted 376 gene flow or migration strategies to maximise local adaptation under climate change. Similarly, SNPs for climatic maladaptation were identified in maritime pine (Pinus pinaster) and validated based on 377 378 differential survival in a common garden trial in an extreme environment (Jaramillo-Correa et al., 2015). 379 These examples illustrate the contribution of genomic applications to predicting natural population 380 responses to climate change and inform MAs for adaptation and mitigation of effects. However, gene-381 targeted MAs, which are often based on the current adaptive state, should be applied with caution in 382 order to preserve sufficient genetic diversity for future unknown threats (Derry et al., 2019; Kardos and 383 Shafer, 2018).

384 **D1.4 Restore and renew diversity**

Restoring terrestrial and aquatic ecosystems provides important ES including climate change mitigation and carbon sequestration (Bastin et al., 2019; Isabel et al., 2020, see also D2.6). Genomic diversity knowledge obtained in keystone species can meaningfully inform MAs on the choice and sampling strategy of population provenances for restoration, leading to more successful establishment and persistence and greater resilience or restored populations (Breed et al., 2019; Gann et al., 2019; Rossetto et al., 2019).

391 Recent restoration MAs for terrestrial ecosystems document a shift from local provenancing to 392 climate-adjusted provenancing (Prober et al., 2015), using landscape genomics methods (see D1.3) 393 to inform seed sourcing and to assess the risks and successes of MAs (Supple et al., 2018). 394 Generalised Dissimilarity Modelling which controls for isolation by distance when testing GEA (Fig. 3) revealed distinct patterns of spatial genomic diversity in five largely co-distributed Acacia species 395 396 supporting provenance regions of different sizes and species-specific seed-sourcing strategies for 397 restoration (Rossetto et al., 2020). In Eucalyptus microcarpa fragmented woodlands of South-eastern 398 Australia, GEA supported climate-based seed sourcing as well as mixed seed sourcing to enhance 399 genetic diversity in revegetation (Jordan et al., 2019, see D2.6). Genetic assessment of reforestation 400 MAs revealed that revegetated sites captured a large proportion of overall genomic diversity (Jordan 401 et al., 2019, 2016). Eucalyptus melliodora is another keystone tree species in many native ecosystems 402 in Australia, some of which are critically endangered. A genomic study in this species showed that 403 restoration projects could source seeds much more broadly (up to ~500 km) than current practice, 404 consistent with recommendations based on phenotypic trait analyses (Supple et al., 2018). This 405 strategy could increase the number of available provenances for restoration, and help enhance the 406 adaptive potential in planted sites.

In the broader context of renewing biodiversity, genomic knowledge is important to monitor the
consequences of assisted re-colonization of species into areas where they were previously depleted,
and also of natural expansion of species into new areas (Berthouly-Salazar et al., 2013; Excoffier et
al., 2009; McInerny et al., 2009; Mueller et al., 2022).

411

412 **D2.** Interacting species genomic diversity for biodiversity and ES management

413 The provision of many ES depends on the complex interaction of species with each other and their 414 environment (Keith et al., 2017; Moreno-Mateos et al., 2020; Pollock et al., 2020). Genomic 415 applications play a key role in elucidating the evolutionary processes affecting communities and 416 species interactions, evaluating their potential effects on biodiversity and ES and can thus inform ES 417 management (Blasco-Costa et al., 2021; Schielzeth and Wolf, 2021; Whitham et al., 2006). The MGs 418 that benefit from genomic information on interacting species include the management of invasives 419 (D2.1), of hybridization (D2.2), of host-microbe interactions (D2.3) and of microbial community diversity (D2.4). Multi-species patterns of genomic diversity in communities also inform the delineation of 420 421 conservation areas (D2.5) and the restoration of communities (D2.6).

422

423 D2.1 Manage invasive species and their effects on species interactions

424 Invasive species are among the biggest threats to biodiversity and ecosystem stability (Simberloff, 425 2013). They interact with their competitors or hosts, may hybridise with related species (see also D2.2), 426 often introduce parasites and pathogens, and may threaten biodiversity and many ES, e.g., material 427 and food production, carbon storage, nutrient cycling, water and air purification (Hamelin and Roe, 2020: North et al., 2021). The process of invasion involves the stages of transport, introduction, 428 429 establishment, and spread (Chown et al., 2015; Hamelin and Roe, 2020). Genomic applications can 430 inform MAs on each of these stages: metagenomic approaches (eDNA or metabarcoding, Fig. 3) are 431 appropriate to detect potentially invasive species, assess invasion risk and inform MAs on prevention 432 strategies in early stages whereas population genomic approaches are suitable to assess the origins. 433 the risks and the drivers of invasion and to monitor its progression so as to inform MAs to limit the 434 spread of invaders and their negative impact on native species, their associated communities and 435 ES (Bouteiller et al., 2019; Chown et al., 2015; Hamelin and Roe, 2020; North et al., 2021).

436 In black locust (Robinia pseudoacacia), a North American native species that invaded Europe in the 437 19th century, SNP data allowed to trace the origin of invasion to a few populations from the 438 northeastern part of the US native range and assign invasion success in Europe to higher clonality 439 (Bouteiller et al., 2019). In the shrub Scotch broom (Cytisus scoparius) in Denmark, a genomic marker 440 study confirmed the invasion by a non-native gene pool and genetic swamping of native vulnerable 441 heathland populations of the same species but the authors cautioned against negative side-effects 442 (e.g., unintended seed dispersal) by removal of the invasive phenotype (Rostgaard Nielsen et al., 443 2016). In some cases removal of genetically identified migrants could minimise such risks.

The raccoon dog (*Nyctereutes procyonoides*) from the *Canidae* family is of East-Asian origin and introduced in Europe for fur trade. It is a host and potential vector for a range of zoonotic diseases including echinococcosis, trichinellosis, rabies and SARS-CoV-2 (Freuling et al., 2020). Genomic information on the origin and spread of invasive populations (see Nørgaard et al., 2017, for an example in Denmark) and marker development from the recently available full genome (Chueca et al., 2021) constitute valuable resources to monitor and control invasive populations and possible associated Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service management. *Biological Conservation* 2023 ;Volum 278. <u>10.1016/j.biocon.2022.109883</u> CC-BY-NC-ND 450 infectious diseases.

451 Genome-wide studies also have the power to pinpoint genes or molecular processes that help 452 understanding the success of an invasive species and develop countermeasures. In the case of the 453 highly invasive house mouse (Mus musculus), island populations in California and in the Galápados 454 lacked rodenticide resistance alleles, which represents an option for population control or 455 eradication (Morgan et al., 2018). In the case of two sister pathogenic tree fungi, introgression from 456 the invasive North American Heterobasidion irregulare into the native European H. annosum increased 457 invasiveness of the latter, suggesting adaptive introgression (Sillo et al., 2021, see also D2.2). 458 Altogether, these studies demonstrate the usefulness of genomic approaches to elucidate and monitor 459 invasion processes and inform MAs for the management of invasives.

460

461 **D2.2 Harness hybridization**

462 Hybridization is a common evolutionary process that may impact all processes of divergence along 463 the speciation continuum (Abbott et al., 2013). Introgression of genes following hybridization can either (i) compromise species survival and integrity by disrupting coadapted gene complexes (Allendorf et 464 al., 2001; Rhymer and Simberloff, 1996), or (ii) increase the adaptive potential of populations, by 465 enhancing diversity and creating novel genetic combinations (Becker et al., 2013; Hamilton and Miller, 466 467 2016; Hoffmann and Sgrò, 2011; Pfennig et al., 2016; Whiteley et al., 2015). Detecting hybrids and characterising introgression and its effects on adaptation is thus directly relevant for conservation and 468 469 natural resource management (Flanagan et al., 2018; Quilodrán et al., 2020). Genomic diversity 470 knowledge in hybrid systems allows to design strategies to monitor hybridization and its effects and 471 as a result, hybridization is being increasingly harnessed as a management tool for genetic rescue 472 or to enhance adaptation or adaptive potential (Chan, 2018; Hamilton and Miller, 2016; Moran et 473 al., 2021; Strait et al., 2021). In this context, the possibility of conserving hybrids should be examined 474 and integrated in novel conservation policies that allow to consider species not as fixed entities but as 475 evolving lineages (Chan et al., 2019; Donfrancesco and Luque-Lora, 2021; Draper et al., 2021).

476 A widely documented case of the use of hybridization for genetic rescue from an imminent threat of extinction is that of the Florida panther (Puma concolor coryi). Release of pumas from the Texas 477 478 subspecies (P. c. stanlevana) increased survival, fitness and heterozygosity and reduced inbreeding 479 depression in the Florida population (see also D1.1), although this MA also illustrated the need of 480 managing infectious disease risks in genetic rescue (Johnson et al., 2010). More generally, 481 understanding the phenotypic effects of introgression, developing cost-effective genotyping tools 482 applicable across a wide range of sample provenances, DNA quantities and qualities is crucial for 483 large-scale monitoring of hybridization and its associated risks, as shown in an assessment of 484 hybridization between wolves (Canis lupus) and domestic dogs (Harmoinen et al., 2021).

In marine ecosystems, coral phylogenies bear a legacy of hybridization, suggesting that introgression
 promoted resilience to environmental changes, e.g., in the genera *Porites, Pocillopora* and *Acropora* Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service
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(Forsman et al., 2017; Willis et al., 2006). For example, genome sequencing in five *Acropora* corals
identified a phylogeny shaped by adaptive introgression and climate change (Mao et al., 2018). Recent
studies confirmed the past introgression events among more than a hundred coral species, some of
them also revealing substantial ecological differentiation despite ancient morphological stasis
(Bongaerts et al., 2021a; Hobbs et al., 2021). These studies support hybridization as a promising tool
for adaptive management in coral reef restoration (Chan et al., 2019, 2018; Rinkevich, 2020).

493 Hybridization has also shaped the genomes of numerous other animal or plant taxa (Margues et al., 494 2019; Suarez-Gonzalez et al., 2018). In the genus Quercus (oaks), introgression has led to the transfer 495 of genetic adaptations between species (Cannon and Petit, 2020; Leroy et al., 2020), suggesting its 496 usefulness in MAs such as assisted gene flow, migration or genetic rescue in the context of adapting 497 forests to climate change, or to disturbed or urban environments (previously developed in D1.2, D1.3) 498 and D1.4, Cannon and Petit, 2020; Hamilton and Miller, 2016; Leroy et al., 2020). Knowledge on gene 499 flow between populations is essential to design such MAs since contact between long-isolated 500 populations might cause outbreeding depression due to incompatibilities in adaptive differences 501 (Aitken and Whitlock, 2013).

502

503 **D2.3 Manage host-microorganism interactions**

504 Global change is associated with deregulation of interactions between host species and their 505 interacting microorganisms, which is projected to disrupt host-symbiont interactions and to increase 506 the frequency of epidemic pest attacks (Bartoli et al., 2016; Mohan et al., 2014). GWAS can address 507 the coevolution of hosts and their associated organisms, and, in the case of pathogens, reveal the 508 genetic basis of host resistance (La Mantia et al., 2013). This is useful to **assess the risks of disease** 509 **outbreaks** and for MAs to **protect hosts from pathogens**, thus contributing to ES by maintaining 510 ecosystem health.

511 In cetaceans, for example, GWAS revealed the genetic bases of adaptation to harmful algal blooms and of resistance to a lethal virus (Batley et al., 2019; Cammen et al., 2015), potentially useful in 512 513 vaccine development (Batley et al., 2019). In plants, provenance and progeny trials (see D1.2) 514 represent opportunities to study interactions between host genotypes and associated organisms. In 515 trees of the genus *Populus*, genes associated with defence chemistry, phenology, growth and insect 516 community composition have been identified (Barker et al., 2019; DeWoody et al., 2013). These co-517 evolutionary interactions between plant genotypes and associated communities can be harnessed to 518 foster plant health, to maintain or increase biodiversity, or to protect endangered species within their environment. It has also been suggested that genomic information on interactions between host plants 519 520 and their symbionts, in particular arbuscular mycorrhizal fungi, can be used to enhance those 521 beneficial associations and restoration success (Aavik et al., 2021).

A promising approach to improve risk assessment for pathogen outbreaks is to examine genomic signatures of host response and pest genetic variability in parallel (Bartoli and Roux, 2017; Karasov Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service management. *Biological Conservation* 2023; Volum 278. <u>10.1016/j.biocon.2022.109883</u>

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524 et al., 2014). This approach can contribute to monitoring the risks or to prevent pathogen spillover from one host to another, as has been shown for an important fungal pathogen at risk of spillover from 525 cultivated apple to the Asian wild apple *Malus sieversii* (Feurtey et al., 2020). If the risk of pathogen 526 spillover to an endangered species is high, discontinuation of host cultivation could be an adapted 527 528 MA. Similarly, genomic assessment of disease spillover risk could be applied to aquaculture and wild 529 fish populations, as a complement to pathogen monitoring (Bouwmeester et al., 2021). Target 530 organisms are *a priori* at higher risk in the case of spillover of new, non co-evolutionary pathogen 531 attacks. In such systems, it is possible to identify genomic regions responsible for so-called exapted, 532 i.e., non co-evolutionary host resistant phenotypes, that would be due to the presence of genes 533 providing broad-spectrum resistance, as has been shown in the oak species Quercus robur 534 (Bartholomé et al., 2020). Although this requires both field work and substantial genomic resources 535 (e.g. mapping populations and a reference genome), rapid progress in non-model species paves the 536 way to more practical applications in the near future (Storfer et al., 2021).

537

538 **D2.4 Conserve and utilise microbial communities in water, soils and sediments**

539 Numerous ES of the Provisioning Section such as agricultural or material production and the 540 Regulation and Maintenance Section such as water guality, reduction of contamination, or nutrient cycling are mediated by microorganisms. In terrestrial and marine environments, microorganisms 541 542 regulate. balance or otherwise affect inter- and intraspecific interactions (Freimoser et al., 2016; Jiao 543 et al., 2014; Marco and Abram, 2019). DNA metabarcoding, metagenomics and metatranscriptomics 544 have been called 'thermometers for biodiversity' as they rapidly provide large data sets on inter- and intraspecific diversity of microorganisms and small organisms from a variety of taxonomic and 545 546 functional groups based on environmental DNA (eDNA) from environmental samples (Breed et al., 2019: Saccò et al., 2022; Wilson et al., 2019). These tools can be applied simply and systematically 547 548 on large geographical scales, their efficiency in detecting species depending on taxonomic groups, 549 sampling conditions and available reference databases (Hua et al., 2015; Ji et al., 2013; Watts et al., 550 2019; Wilson et al., 2019).

551 In forests, wood decomposition by microorganisms, in particular by saprophytic fungi, is crucial for ES 552 such as nutrient recycling, carbon sequestration, soil formation, habitats creation and the preservation 553 of the diversity of organisms living in dead wood (Tedersoo et al., 2016). DNA metabarcoding of forest 554 soils showed the impact of distinct keystone forest tree species, edaphic variables and past forest 555 management on microorganisms community structures (Behnke-Borowczyk et al., 2021; Jamy et al., 2020; Tedersoo et al., 2016). This knowledge can inform forest management on which tree species 556 557 are most appropriate to maximise soil functions such as carbon sequestration and nitrogen 558 storage and to preserve soil microorganism diversity and their derived ES (Fig. 2). For example, 559 shotgun metagenomic sequencing revealed that soils under Prunus serotina exhibited functions that 560 indicate a rapid nitrogen cycle and a high inorganic nitrogen availability (Kelly et al., 2021), suggesting 561 that P. serotina can be used for soil reclamation in nitrogen-poor soil conditions (e.g. in coal mine

562 spoil heaps) to **restore post-industrial ecosystems** (see also D2.6). More generally, metagenomics 563 and metatranscriptomics can inform on the response of microorganism communities to environmental 564 change and identify mutualistic endophytic and rhizosphere plant-microbial associations, which opens 565 possibilities to harness these microbial functions through MAs (changing plant cover, inoculation) to 566 support desired responses (Hamilton et al., 2016; Jansson and Hofmockel, 2020).

eDNA approaches are also increasingly applied in aquatic environments (Pawlowski et al., 2018;
Saccò et al., 2022; Wang et al., 2021). For example, functional metagenomics can refine microbial
community profiles associated with specific water masses at different depths that support different ES
(Keuter et al., 2015; Lam et al., 2015).

571

572 C2.5 Delineate areas for conservation and ES

573 Delineating priority areas for biodiversity conservation and ES is a common challenge for managers 574 (Hermoso et al., 2018; M. Jung et al., 2021; Mokany et al., 2014; Sala et al., 2021; Weeks and Adams, 575 2018). Traditional approaches for conservation prioritisation identified hotspots based on species richness and endemism (Mittermeier et al., 2005; Myers et al., 2000). Recent approaches use multiple 576 577 criteria to optimise the spatial representation and conservation of multiple biodiversity levels or 578 ecosystem properties, while also minimising socio-economic limitations (Carvalho et al., 2017, 2016; 579 V. Jung et al., 2021; Moilanen et al., 2009; Morán-Ordóñez et al., 2018; Pollock et al., 2020). Genomic 580 applications can facilitate spatial prioritisation through informing on drivers and features of 581 biodiversity representation and persistence (D2.4) and on adaptive population management (Andrello et al., 2022; Hohenlohe et al., 2021; Nielsen et al., 2022), thus contributing to ecosystem resilience 582 583 and regulation (Des Roches et al., 2021; Raffard et al., 2019, see also D1). When combined with spatially explicit measures of ES supply, demand and flow, genomics-informed conservation 584 585 prioritisation can help resolve trade-offs between different management objectives for biodiversity 586 conservation and different provisioning and/or maintenance and regulation ES (Hermoso et al., 2018; 587 M. Jung et al., 2021; Law et al., 2021; Pereira et al., 2020; Sala et al., 2021; Villarreal-Rosas et al., 2020), thus maximising benefits of biodiversity and ES. 588

589 The body of research on genetic diversity across diverse species and evolutionary timescales 590 suggests that multi-species conservation objectives are necessary to delineate protected-area 591 networks that preserve evolutionary processes at the species and community levels (Carvalho et al., 592 2017; Nielsen et al., 2017). Genomic data provide such metrics and enable the robust delineation of 593 conservation areas that can be adjusted to desired MGs with regard to population adaptation or to 594 maximise multispecies evolutionary potential (Phair et al., 2021; Xuereb et al., 2021). A study on 595 six freshwater fish species suggested maximising the representation of individual alleles (Paz-Vinas 596 et al., 2018) while another on three amphibian species recommended maximising the representation 597 of both neutral and adaptive allele clusters (Hanson et al., 2020). In aquatic ecosystems multispecies 598 information from metabarcoding is increasingly applied in spatial planning (Bani et al., 2020; 599 Pawlowski et al., 2018). Although still rare, the application of genomic multi-species assessments for Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service management. Biological Conservation 2023 ;Volum 278. 10.1016/j.biocon.2022.109883 CC-BY-NC-ND

- 600 protected area delineation are increasingly relevant for conservation planning and climate-adaptive 601 management of communities (Gaitán-Espitia and Hobday, 2021).
- 602

603 D2.6 Restore communities, habitats and ecosystems

The large-scale restoration of converted or degraded ecosystems is primordial to mitigate climate change and limit species extinction world-wide (Rey Benayas et al., 2009; Strassburg et al., 2020; Suding et al., 2015). Restoration success will strongly depend on defining specific, pertinent and achievable MGs (see B2, Coleman et al., 2020; Coleman and Bragg, 2021). These will aim to restore the biodiversity of a historical or extant reference state to renew forfeited ES (Breed et al., 2019; Suding et al., 2015), or, alternatively, to reinforce or redefine the community for biodiversity conservation and ES provisioning under future conditions (Coleman et al., 2020; Kleypas et al., 2021).

611 Restoration of habitats, communities or ecosystems first depends on the restoration success of 612 keystone species (see D1.4). Genomic applications in keystone and associated species allow to 613 select provenances adapted to the current or future predicted climate, to assess the risks 614 associated to their use in restoration in terrestrial or aquatic environments, and to monitor genetic 615 diversity in the restored populations (D1.4, Breed et al., 2019; Coleman et al., 2020; Rossetto et al., 616 2019; Wood et al., 2020). A scientifically supported strategy for restoration of resilient communities is 617 regional admixture provenancing based on mixing seeds of a locally adapted provenance with that 618 of a few surrounding provenances which contributes to increasing the diversity for future adaptation, 619 as implemented jointly for multiple species in the restoration of European mesic grasslands 620 (Bucharova et al., 2019). In this approach, provenance regions are defined based on the abiotic 621 environment and are the same for all species (Bucharova et al., 2019). Multispecies regional 622 admixture provenancing could benefit from species-specific genomics-based delineation (Rossetto 623 et al., 2020) to facilitate reaching a compromise between current adaptation and the need for future 624 adaptive potential of restored communities (Bucharova et al., 2019). A study that combined genomic, 625 phenotypic and environmental data concluded that local provenances were the most appropriate to 626 restore moderately disturbed sites, whereas provenance admixture was found to be most effective for 627 the restoration of highly degraded sites (Carvalho et al., 2021; Rico, 2021). Monitoring the genetic 628 outcomes of restoration strategies allows management practices to evolve as knowledge 629 accumulates (Hodgins and Moore, 2016).

630 In marine ecosystems, the use of genetics has been identified as a priority in reef restoration (Kleypas 631 et al., 2021; Vardi et al., 2021), where MAs such as assisted migration of multiple species may create novel species assemblages (sensu Rinkevich, 2015) and dynamics, and in effect, lead to assisted 632 633 translocation of communities (Rinkevich, 2021). The recent development of 'reefscape genomics' 634 approaches that combine genomic data with state of the art spatial mapping and mass phenotyping 635 paves the way for fine-scale landscape genomic approaches on coral reefs and other marine 636 ecosystems, facilitating the characterization of evolutionary processes that provide guidance and 637 monitoring tools for coral reef restoration (Bongaerts et al., 2021b).

638 Metagenomic and metatranscriptomic applications can monitor the species composition, the desired 639 species interactions and the metabolic pathways necessary to deliver the targeted ES in restored 640 ecosystems (Breed et al., 2019; Cordier et al., 2021). New biotechnology techniques, in particular 641 the CRiSPR-Cas9 system (Hsu et al., 2014), bring the possibility to manipulate and edit genetic 642 material in a rapid fashion. While sometimes controversial, such biotechnological tools can tackle 643 urgent conservation and ES challenges by introducing precisely the desired traits into an original 644 genetic background (Breed et al., 2019; Segelbacher et al., 2022). Key restoration species can be 645 targeted with fitness-improving gene edits while pests can be controlled with suppression gene edits 646 that cause infertility or lethality (Breed et al., 2019). Another biotechnology application is chimerism. 647 the assembling of entities that possess cells of two or more conspecifics, which may help to accelerate 648 adaptation of corals in restoration (Rinkevich, 2021). However, before application of biotechnology for 649 restoration, a careful risk assessment on a case-by-case basis is needed, including technical, ethical 650 and political aspects (Breed et al., 2019, Segelbacher et al., 2021).

651

652 E. Discussion

653 We have identified through a keyword search in the scientific literature that there is a gap in 654 recognizing, addressing and discussing the use of genomics for biodiversity conservation and 655 management of ecosystem services (ES). Further, examining the scientific literature on specific 656 genomic applications pertaining to specific management goals, we found that there was also an 657 application gap. Indeed, we show with case studies that: Genome-wide genetic marker approaches 658 are mostly limited to keystone or flagship species such as iconic animals (e.g., the hihi, bat species), 659 top predators (e.g., the Iberian lynx, the Florida panther) or habitat-shaping and economically important tree species (e.g., pines, spruces, oaks). Although approaches on more modest numbers of 660 661 genetic markers are more common and remain useful especially to capture neutral genetic variation 662 (Fig. 3), genomic approaches are not yet widely applied, i.e., mainstreamed into biodiversity 663 conservation and ES management. The outlook for such mainstreaming is favourable: we are at the beginning of an exponential stage of data gathering on whole genomes of species and genomic 664 665 variation across populations and, additionally, we are increasingly accessing genomic information from 666 historical or ancient DNA samples for a temporal, holistic insight into eco-evolutionary processes 667 (Jensen et al., 2022). We summarise below our findings on genomic applications for natural resource 668 management, we discuss the ambitious scientific and management goals they allow to tackle and the 669 policy and management contexts and developments that will enable their most effective use.

670

671 E1. Genomics applications allow to tackle ambitious management goals

We showed that genomics can significantly improve the design of management actions to meet
 specific management goals of interest to natural resources managers. These include goals on
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674 biodiversity conservation and restoration as well as multifaceted goals on sustainable productivity and 675 provision of ES under environmental changes and anthropogenic stressors. Genomic applications help to solve trade-offs between different management objectives, and inform decision making to 676 maximise the long-term sustainable provision of ES (Hermoso et al., 2018; M. Jung et al., 2021; Law 677 et al., 2021; Pereira et al., 2020; Sala et al., 2021; Villarreal-Rosas et al., 2020). Usually, such goals 678 679 are intrinsically interconnected. We chose to organise them separately on purpose to visualise and 680 exemplify possible management options unambiguously to ecosystem managers. We deliberately 681 included several application examples in this review to illustrate the power of genomic information, 682 including functional genetic and potentially adaptive variation, in species and communities. Beyond 683 approaches that focus on single species, promising novel applications for genomics in biodiversity and ES management clearly lie in using its power to exploit species interactions. Introgression of adaptive 684 685 variation from closely related populations or species can enhance the resilience of populations after 686 only a few generations of natural selection, while preserving the adaptive potential of the recipient 687 population (Hamilton and Miller, 2016; Leroy et al., 2020). Managing the co-evolutionary diversity of 688 species interactions with their symbionts or key pathogens can support ecosystem health for the 689 sustainable provision of ES (Aavik et al., 2021; Feurtey et al., 2020). Finally, managing microbial 690 function in terrestrial and marine ecosystems has the power to increase crucial ecosystem functions 691 such as carbon storage (Jansson and Hofmockel, 2020; Pawlowski et al., 2018; Saccò et al., 2022).

692

693 E2. Genomics applications or alternative approaches: how to choose?

694 It should be pointed out that the necessary evolution-based management actions do not always require 695 molecular genetic or genomic data (Hoban et al., 2020). A careful examination of the management 696 problem and available resources will help to identify the most appropriate data strategy, for example, 697 (1) to use proxies such as census population size to assess effective population size (Hoban et al., 698 2020; Hoban et al., 2021b), (2) to use phenotypes to assess short-term responses to selection based 699 on quantitative genetics (Alexandre et al., 2020) or (3) to use an effective strategy to obtain the most 700 appropriate genetic or genomic data in pertinent species or communities (see B2, Angeloni et al., 701 2012; Blasco-Costa et al., 2021; Flanagan et al., 2018; Schielzeth and Wolf, 2021). It should also be 702 stressed again that it is precarious to focus on current genetic adaptations alone to foster the future 703 persistence and resilience of populations. This is because 1) even if major effect loci can be found for 704 a trait of interest in a particular population, promoting them in another environment can have neutral 705 or even negative effects because complex adaptive traits are highly polygenic and thus phenotypes 706 depend on a given genomic background which can respond to different environments in different ways 707 due to genotype by environment interactions (Lind et al., 2018), and 2) there is uncertainty as to what 708 future environmental conditions will be. In the case of MAs that involve moving genetic materials 709 (individuals, populations, communities) or confronting them with new environments through 710 environmental change, the best assurance for future adaptability is to preserve and foster high genetic 711 diversity (Derry et al., 2019; Kardos and Shafer, 2018).

712 Epigenetic variation may also offer applications to the benefit of ES management. Transgenerational Heuertz, Myriam et al 2022. The application gap: Genomics for biodiversity and ecosystem service management. *Biological Conservation* 2023 ;Volum 278. <u>10.1016/j.biocon.2022.109883</u> CC-BY-NC-ND 713 epigenetic and novel epigenetic landscapes may help predict adaptive responses through their effects 714 on phenotypes and thus the fitness of organisms (Jeremias et al., 2018). The dynamic epigenetic 715 system, in interaction with the environment, can thus direct genetically determined natural selection 716 (Manjrekar, 2017). As a consequence, epigenetic processes can support fast intraspecific adaptation, 717 impacting ecosystem services and functions (McCaw et al., 2020; Rey et al., 2020). Although 718 epigenetic variation and processes appear to strongly vary across species with regard to their 719 frequency and type of responses to climate change (McCaw et al., 2020), they can collectively impact 720 important ES and their study is just beginning in non-model species.

721

722 E3. Genomic applications in the natural resource policy context

723 Adopting effective biodiversity conservation and management for ES is urgent and necessary in the 724 current biodiversity crisis, and genetic and genomic methods and data are ready to be implemented 725 to support the most effective management as we show in this paper (see also Hoban et al., 2020; 726 Hoban et al., 2021a; Laikre et al., 2020). In this context, it is especially important that the CBD post-2020 Global Biodiversity Framework adopt a strong goal for the conservation of genetic diversity, and 727 728 genetic diversity indicators to monitor progress towards achieving this goal (Hoban et al., 2020; Hoban 729 et al., 2021a). Genetic and genomic approaches are also crucial to improve management for the 730 implementation of policies that are already in place, for biodiversity conservation and provision of ES 731 as well as for human well-being, such as the UN 2030 sustainable development goals, and the EU 732 Biodiversity strategy for 2030. For example, genomics can help decide which species and 733 provenances are the most suitable for major ongoing tree planting initiatives, such as the '3 Billion 734 Trees Pledge' committed by the EU biodiversity strategy for 2030 under the EU Green deal, and its North American counterparts, the '1 trillion tree initiative' in the USA and the '2 billion trees 735 736 commitment' in Canada. Genomic applications will also support a faster implementation of sustainable fishing practices regulated by the EU Common fisheries policy and the Marine Strategy Framework 737 738 Directive. Long-term natural resource planning and policy requires genetic diversity and gene flow 739 information in increasing numbers of species to reach the best management decisions without 740 compromising the resilience and adaptive potential of ecosystems (G-BIKE, 2020). Novel 741 developments and adaptations of the policy framework will be necessary to allow for ambitious MGs 742 to adapt natural resources to future needs. For example, legal recognition of hybrids in conservation 743 and natural resource policies would make a significant step forward to enhance such MGs, recognizing 744 that species are not fixed but evolving entities (Draper et al., 2021; Fitzpatrick et al., 2015). Other 745 ambitious policy developments that genomic data can support through proposing consensus methods 746 concern the taxonomic delimitation of closely related species in species complexes (Coates et al., 747 2018) and the conservation of adaptive potential (Funk et al., 2019).

748

749 E4. Genomics applications in natural resource management in practice

750 The scientific community is increasingly well organised, in conjunction with natural resource managers, to use the most powerful scientific knowledge to promote and achieve ambitious goals for biodiversity 751 in policy and practice, e.g., through collaborative instruments such as the EU COST Action G-BIKE 752 753 (Genomic Biodiversity Knowledge for Resilient Ecosystems, G-BiKE, 2019) or the Coalition for 754 Conservation Genetics that federates four eminent organisations (Kershaw et al., 2022). Scientists 755 increasingly recognize the power of genome-wide data for monitoring and managing genetic diversity 756 (e.g., Meuwissen et al., 2020), with the great promise of mitigating the ever intensifying environmental 757 change. At the same time, natural resource managers are increasingly aware of the benefits provided 758 by genomic monitoring tools, and teaming up with geneticists for timely interventions and optimising 759 ES. There remains a need to enhance standardisation and simplification of genomic data acquisition 760 and analysis workflows to reduce the cost, increase the speed and facilitate the practical deployment 761 of genomics in MAs (Rossetto et al., 2021; von Thaden et al., 2020). Synergies between scientists 762 and ES managers need to be increasingly fostered not only at international (Kershaw et al., 2022) but also national and local levels to bridge the science-ES management application gap. Ambitious goals 763 764 for biodiversity conservation, its sustainable use and provision of ES can be achieved by merging the 765 high level of expertise required to analyse the genomic data and the expertise of real-world ES 766 management using appropriate workflows, deploying genomics training to ES managers, and 767 incorporating indigenous and local knowledge into science-informed MAs (e.g., Díaz et al., 2020). In COST Action G-BIKE we follow this rationale, and in this work in particular, we prepared a "Brief for 768 nature managers" (Supplementary material S2) that summarizes our main findings and provides 769 770 application examples targeted to biodiversity and ES managers. The brief will be made available on the G-BIKE website (https://g-bikegenetics.eu/) in a user-friendly layout with illustrations and 771 772 translated to several languages for dissemination. Another example framework for science-informed 773 biodiversity and conservation actions on the ground is the Biodiversity and Ecosystem Services 774 Network (BES-Net) that builds capacity and commitment for biodiversity action across the world by translating the latest IPBES products into action, but BES-Net still lacks the implementation of 775 776 genomics. Governments and natural resource managers need to embrace the huge potential of genomics for ES, particularly in this time of rapid changes in our ecosystems as a result of 777 778 anthropogenic effects.

779

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796 Declaration of interests

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804 **F. References**

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1619 Author contributions

- 1620 Conceptualization: MH, PGG, JAMR, SBC, JG, BR, PR, TG, BJM, ST, AVa, AVe
- 1621 Data curation: MH, TG, PGG
- 1622 Formal analysis: MH, TG, PGG
- 1623 Funding acquisition: SH, CV
- 1624 Investigation: MH, PGG, SBC, JG, BR, PR, TG, JAMR, ST
- 1625 Methodology: PGG, MH, SBC, JG, BR, PR, TG, JAMR, ST
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- 1627 Resources: CV
- 1628 Visualisation: JMIB, PGG, MH, JG, ST, BR
- 1629 Roles/Writing original draft: MH, PGG, SBC, JG, BR, PR, TG, JAMR, ST, AVa, SCGM, IP, AVe
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- 1631 BJM, IP, JAMR, ST, AVa, AVe, CV
- 1632 1633

1634 Supplementary materials

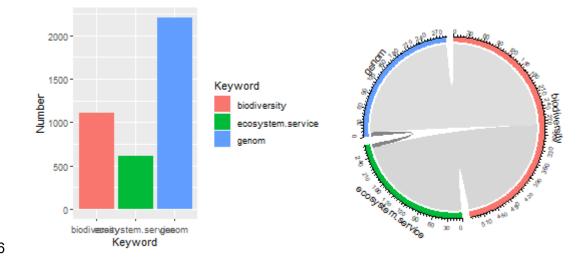
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S1 Keyword analysis - How does genomics link to ecosystem services in the scientific literature?

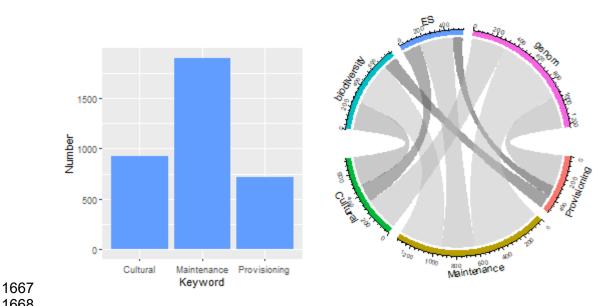
1638 To systematically and quantitatively examine the links between the concepts of genomics, biodiversity 1639 and different types of ecosystem services in the scientific literature, we assessed and analysed the 1640 co-occurrence of keywords attributed to these concepts in the abstracts of published articles.

1642 Methods We conducted terminology research Pubmed Central а on (https://www.ncbi.nlm.nih.gov/pmc/) for pairwise combinations of the terms "biodiversity", "ecosystem 1643 service" and "genomics" in the body text of articles on October 8th, 2020, using the "Advanced search" 1644 tools. The search command was formulated as "(ecosystem service[Body - All Words] AND 1645 biodiversity[Body - All Words]) OR (ecosystem service[Body - All Words] AND genomics[Body - All 1646 1647 Words]) OR (biodiversity[Body - All Words] AND genomics[Body - All Words])". Abstracts of all 1648 retrieved papers were searched with 1. Target keywords ("ecosystem service", "genom" and "biodiversity"); 2. Keywords or combinations of keywords describing ES Classes belonging to the three 1649 1650 ES Sections Provisioning ES, Regulation and maintenance ES, and Cultural ES, as defined by the Common International Classification of Ecosystem Services, v5.1 available at https://cices.eu/. CICES 1651 1652 classifies ES in a system of four hierarchical levels, 1) Sections, 2) Divisions, 3) Groups, and 4) 1653 Classes. We attributed each retrieved paper to one or more Classes (four-number code of CICES) 1654 based on keywords found in the abstract that matched the corresponding CICES Class descriptions. 1655

1656 Results - Our keyword research yielded 6417 references, the earliest published in 1993; 6064 papers 1657 had an abstract and were analysed. The target keywords "biodiversity", "ecosystem service" and 1658 "genom" appeared in the abstracts of 2211, 616 and 1114 retrieved papers, respectively, representing 1659 a total of 2871 papers (Figure S1). We discovered that only 9 papers mentioned "genom" (contained 1660 in genome, genomic, genomics) and "ecosystem service" simultaneously in the abstract although both concepts are well connected through biodiversity (Figure S1). The links between the keywords 1661 1662 "genomics" and "ecosystem services" appear poorly exploited in the literature, but the strong connection of both concepts with biodiversity illustrates that there is potential of genomic studies for 1663 1664 ES valuation. 1665



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1669 Figure S1. Articles retrieved in a search on Pubmed Central (https://www.ncbi.nlm.nih.gov/pmc/) for pairwise combinations of the terms "biodiversity", "ecosystem service" and "genomics" in the body text 1670 1671 of articles, on October 20, 2020.

1672

1673 A total of 2871 papers were attributed to specific ES Sections, 720 to the Provisioning Section, 1903 1674 to the Regulation and Maintenance section and 929 to the Cultural Section (Figure S2); multiple 1675 attributions were possible. The "genom" term was associated with articles from the three Sections in 1676 proportions similar to the number of articles retrieved.

1677 Within the Provisioning ES Section, the retrieved papers were unevenly distributed across Classes:

1678 Studies on plants as food crops (1.1.1.1) or for materials (1.1.1.2) were represented about four times

1679 more frequently than such studies on animals (1.1.3.1 and 1.1.3.2). Genetic resources as materials for breeding (1.2.1.2, 1.2.2.2, 1.2.2.3) or population conservation (1.2.1.1, 1.2.2.1) were also well 1680 represented (see Supplementary material). 1681

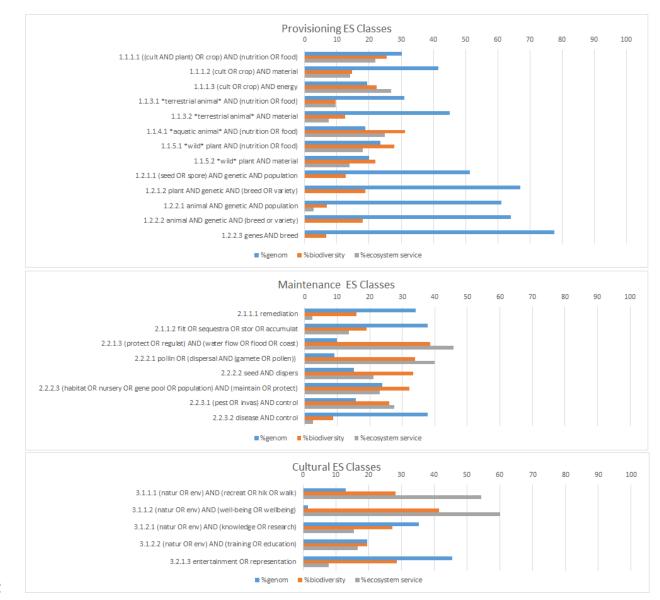


Figure S2. Attribution of articles with the target keywords "biodiversity", "ecosystem service" or "genom" appearing in their abstracts to Sections and Classes of Ecosystem Services as defined by CICES. Only classes with more than 30 attributed studies are represented.

In the Classes of the Provisioning Section with more than 30 studies represented (Figure S2), we illustrate the percentage of studies in which our target keywords occurred in the abstract. The "genom" term occurred in over 50% of the studies on breeding or population establishment or conservation (1.2.1.1., 1.2.1.2, 1.2.2.1, 1.2.2.2, 1.2.2.3), and was more frequent in classes on food (1.1.1.1, 1.1.3.1) and materials (1.1.1.2, 1.1.3.2) than energy (1.1.1.3). The ecosystem service term was, strikingly, very poorly represented in these Classes on breeding or conservation, suggesting that studies on the provision of genetic materials or resources are not commonly presented as targeting an ES. The

biodiversity term was mentioned as the most frequently associated keywords in Classes on fisheries (1.1.4.1) or wild-sourced food or materials (1.1.5.1, 1.1.5.2). When characterizing genetic materials using genomic tools, scientists are fulfilling a Provisioning ES, a link that could be made more visible in future genomic studies.

1697 In the Regulation and Maintenance ES Section, the retrieved studies were attributed to Classes in a strongly uneven way, with a strong overrepresentation of studies attributed to the Class on filtration, 1698 sequestration, storage or accumulation (2.1.1.2) and a near-absence of studies in the Classes that 1699 1700 focus on the contribution of living organisms in the regulation of soils (2.2.4.x, 2.2.5.x). The "genom" 1701 term (Figure 2B) was mostly associated with bioremediation (2.1.1.1), filtration / sequestration / 1702 storage / accumulation (2.1.1.2) and disease control (2.2.3.2). These Classes are much less 1703 associated with the ES term, and thus not explicitly valued as ecosystem services. Genomics was little 1704 associated with water flow regulation (2.2.1.3), and perhaps, unexpectedly, with pollen or seed 1705 dispersal (2.2.2.1, 2.2.2.2) and control of invasives (2.2.3.1). The latter categories are strongly associated with the biodiversity and ES terms though, and thus correctly valued as such in the 1706 1707 literature.

1708

1709 In the ES Section on Culture, most retrieved studies were attributed to the Class on nature-related 1710 knowledge or research (3.1.2.1), and accessorily to the one on nature-related training or education 1711 (3.1.2.2); Classes on nature-related experiences and wellbeing (3.1.1.1, 3.1.1.2) or entertainment and 1712 representation (3.2.1.3) were also significantly represented (> 30 studies/ Class; Flgure 2C). Classes 1713 related to natural heritage, aesthetic, spiritual or religious experiences were little represented. 1714 Genomics was predominantly associated with the class on nature-related knowledge or research 1715 (3.1.2.1) and that on representation (3.2.1.3), although the latter could be an artifact due to multiple 1716 meanings of the term "representation": genomics was little associated with nature-related experiences 1717 and human well-being (3.1.1.1, 3.1.1.2), although the latter classes are clearly associated with 1718 biodiversity and ecosystem services.

Our keyword analysis on the terms genomics, biodiversity and ecosystem services in the scientific literature has limitations, especially due to the fact that the words used to define ES classes can have multiple meanings and that CICES categories are unevenly covered in the scientific literature. The analysis allows us to conclude that the link between genomics and ecosystem services is exploited in breeding and biodiversity conservation studies, but that there is potential for genomics studies in other fields to highlight more clearly their contribution to ES.

- For Provisioning ES, the genomic characterization of materials can be better promoted as an
 ES.
- For Regulation and Maintenance ES, genomic studies relating to bioremediation, filtration,
 sequestration, storage or accumulation and with disease control have potential to be better
 values as delivering ES.
- For Cultural ES, genomic applications are not much represented beyond knowledge
 generation, thus there is no clear potential identified to value them as ES.

To better exploit this link, researchers could use a multidirectional approach based on 1. identifying the ES that match the object of their genomic work, instead of using biodiversity-centered approach only; 2. targeting genomic studies toward ES that have received little contributions from genomics but where a potential may exist, through including genome-ES studies into existing and future projects and programmes.

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S2 Brief for nature managers - Genomic applications for the 1738

conservation and management of biodiversity and ecosystem 1739

services 1740

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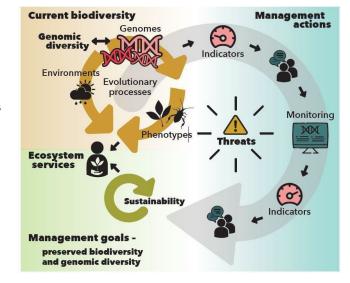
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- 1742 The ongoing loss of biodiversity impacts ecosystem services (ES), the benefits that ecosystems • 1743 provide to people (e.g., pollination, timber production, water filtration)
- 1744 High biodiversity within species, i.e., genetic diversity, allows populations and species to adapt and be resilient in the long-term 1745
- 1746 Long-term resilient communities yield sustainable ES
 - Nature managers can use genetic diversity information to more effectively
 - achieve biodiversity conservation and sustainable nature management goals 0
 - 0 comply with biodiversity policies



1753 WHY AND HOW – Collaboration with scientists 1754 can provide genetic or genomic diversity 1755 knowledge (BOX) that benefits nature managers 1756 to:

- 1757 Design management actions based on • genetic indicators to meet their ES goals 1758
- 1759 Monitor the success of implemented • management actions 1760
- 1761 Adjust management actions as necessary . 1762 to achieve sustainability

Provisioning

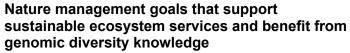
Food, materials,

resources

Ecosystem

services

following CICES v5.1



- Conservation of threatened species and delineation of conservation/management areas
- Management
 - o for sustainable productivity
 - for adaptation to climate change
 - of invasive species
 - of host-microbe interaction, e.g., pest control, 0 symbionts
 - o of microbial communities
 - o for ES derived from water, soils and sediments

Outdoor recreation, intellectual Species, habitat and ecosystem restoration or symbolic interactions with gap: Genomics for biodiversity and ecosystem service events, pollution

management. Biological Conservation 2023 ;Volum 278. 10.1016/j.biocon.2022.109883 CC-BY-NC-ND

• Implementation of new biodiversity policies

BOX: Genetic diversity is the intraspecific diversity between individuals within a species, encoded in DNA and expressed in diverse phenotypes and adaptations to environments.

Genetic diversity

- Determines species' adaptive potential to environmental change,
- Increases ecosystem resilience in the face of climate change and anthropogenic risks,
- Supports all the other levels of biodiversity that deliver ecosystem services, benefiting people

Genomic diversity refers to genetic diversity measured at hundreds to millions of DNA sites spread across the genome. It provides highly detailed information on

- Genetic diversity and inbreeding within populations
- Genetic structure among populations
- Species' past demographic and selection history
- Genes involved in adaptive variation and adaptive potential
- Genomic signatures of hybridization

WHICH DATA - Genomic diversity information to support management can be collected

- in a species threatened by extinction
- in the species most relevant for the ecosystem function or service of interest
- in interacting species, e.g., invasive species, hybrids, host-pest systems
- in a community of microbes

Management goals	Genomics-informed management actions		
Population or species	reduce inbreeding to prevent inbreeding depression, preserve gene		
conservation	pools, assist colonisation, design conservation areas that maximise		
	adaptive potential		
Sustainable productivity	identify populations (stocks) for management, breed for/promote		
	productivity while conserving genetic diversity		
Climate adaptation	favour adaptive alleles while conserving genetic diversity, assisted		
	gene flow, assisted colonization		
Restoration	perform climate-adjusted provenancing while conserving genetic		
	diversity		
Pest control	monitor disease dynamics, identify and promote co-evolved		
	resistance, prevent pest spillover		

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	-	 characterise community function and manage it, e.g., through associated vegetation or inoculation to promote desired properties identify alien species to prevent invasion, identify invasive genotype 					
Control of inv	asives identify alien spe						
•	PRACTICE, NATURE MANAGERS CAN						
	ate with scientists on data, methods and implementation of new policies the need for genomic data, its collection and use for a given management goal						
	genomic information to identify risks of management options, including inaction						
-							
management							
о е.д., і	isks of co-translocated pathoger	ns in the case of tran	slocation or population				
suppl	blementation						
•	nt the best genomics-informed management actions and monitor their risks and						
successes	3						
Examples of §	Examples of genomic applications for nature management						
Illustration	Genomic applications help	Illustration of	Including information on				
of Atlantic	to secure the future of	a bat of	adaptive genomic variation ir				
cod	<u>seafood.</u> Genomic	genus <i>Myotis</i>					
	applications revealed the		species distribution modelling				
	applications revealed the geographic distribution of		species distribution modelling improves projections for futur				
			species distribution modelling improves projections for futur				
	geographic distribution of		species distribution modelling improves projections for futur range losses and the potentia for population rescue using				
	geographic distribution of distinct Atlantic cod		species distribution modelling improves projections for futur range losses and the potentia for population rescue using				
	geographic distribution of distinct Atlantic cod ecotypes and the genome		species distribution modelling improves projections for futur range losses and the potentia for population rescue using population genetic connectivi				
Illustration	geographic distribution of distinct Atlantic cod ecotypes and the genome regions responsible for their	Illustration of	species distribution modelling improves projections for futur range losses and the potentia for population rescue using population genetic connectivi				
of	geographic distribution of distinct Atlantic cod ecotypes and the genome regions responsible for their differential adaptation. <u>Genomics-informed</u> provenancing strategies for	Illustration of a pine	species distribution modelling improves projections for future range losses and the potentia for population rescue using population genetic connective or assisted colonization.				
of Australian	geographic distribution of distinct Atlantic cod ecotypes and the genome regions responsible for their differential adaptation. <u>Genomics-informed</u> provenancing strategies for woodland restoration that	Illustration of	species distribution modelling improves projections for future range losses and the potentia for population rescue using population genetic connective or assisted colonization. <u>Monitoring of gene flow from exotic plantations into native</u> <u>relict stands of Mediterranea</u>				
of Australian Acacia	geographic distribution of distinct Atlantic cod ecotypes and the genome regions responsible for their differential adaptation. <u>Genomics-informed</u> provenancing strategies for woodland restoration that account for the drivers of	Illustration of a pine	species distribution modelling improves projections for future range losses and the potentia for population rescue using population genetic connective or assisted colonization. <u>Monitoring of gene flow from</u> <u>exotic plantations into native</u> <u>relict stands</u> of Mediterranear conifers demonstrated that the				
of Australian	geographic distribution of distinct Atlantic cod ecotypes and the genome regions responsible for their differential adaptation. <u>Genomics-informed</u> provenancing strategies for woodland restoration that	Illustration of a pine	species distribution modelling improves projections for futur range losses and the potentia for population rescue using population genetic connectivit or assisted colonization.				

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to established seedlings. Exotic pollen did not lead to fitness

reduction in offspring in native

stands.

future climates than

strategies based on

species.

distribution similarity of tree

	Illustration of one of the pest species or leaf lesions	Genomic biosurveillance of tree pathogens and pests can be reliably conducted on plant lesions, even <i>in situ</i> in remote forests, allowing for fast and accurate	Illustration of an abandoned mining site	Metabarcoding of soil microbial communities informs on the effectiveness of soil reclamation activities, as shown on the site of an abandoned iron and sulfur				
	from the	identification that can speed		mine in southern Poland where				
	paper	up management		soil restoration measures were				
		interventions.		conducted in the 1970s.				
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1809	• the EU Habitat directives,							
1810	 the EU Natura 2000 network management, 							
1811	 the CBD Post-2020 global biodiversity framework, 							
1812	 the UN 2030 sustainable development goals, 							
1813	• the EU 2030 Biodiversity strategies,							
1814	• the EU Forest strategy for 2030,							
1815	 the EU Green deal and infrastructure strategy, 							
1816	the EU Water Framework Directive,							
1817	 the EU Common fisheries policy and Marine Strategy Framework Directive 							
1818								
1819	The content of this brief for nature managers is based on research published in Biological Conservation and							

- 1820 developed by COST Action G-Bike (Genomic biodiversity knowledge for resilient ecosystems) under working
- 1821 group 3 Genomics and ecosystem services <u>https://g-bikegenetics.eu/en</u>



