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Letter to the editor

Effective population size remains a suitable, pragmatic indicator of genetic diversity for all species, including forest trees

Fady & Bozzano highlight some challenges to a proposed Convention on Biological Diversity (CBD) indicator of genetic diversity based on effective population size, Ne (Hoban et al., 2020). We appreciate the thoughtful debate and concur that genetic diversity indicators must be reliable and scalable. We fully agree that “genetic diversity should be better considered in the CBD post-2020 framework to prevent the irreplaceable loss of biodiversity… existing indicators are far from satisfactory.” As Fady & Bozzano state, Ne is essential for monitoring vital aspects of genetic diversity: loss of genetic diversity due to drift (genetic erosion), inbreeding rate (genetic health), and potential for adaptation and long term survival (resilience).

Drawing on examples for forest trees, Fady & Bozzano argue that: Ne > 500 is not applicable to all species because small populations are not necessarily at risk of genetic diversity loss; estimating Ne and defining populations can sometimes be difficult; and use of a general rule Ne/Nc ratio of 0.1 obscures variation among taxa. They suggest that the Ne threshold should be taxon-specific, taking into account biological features of the taxon; and that recent EUFORGEN indicators are valuable for tracking tree genetic diversity. These are important considerations, but we argue that none of them invalidate our proposed indicators.

Ne > 500 is an appropriate, well-accepted threshold for maintaining genetic diversity in diverse organisms, even trees. It is used by EUFORGEN for genetically at-risk forest units (eufgis.org), by the U.S. Fish and Wildlife Service for delisting endangered species (idfg.idaho.gov/species/bibliography/1500634), and by FAO for assessing genetic erosion in threatened animal breeds (fao.org/3/i3327e/i3327e00.htm). Of course, some plant populations have high genetic diversity and no inbreeding despite low Ne (Silva et al., 2020). Trees may tolerate low Ne because of their biology- somatic mutations are transmitted to offspring (unlike in animals), trees are often highly outcrossing, and many trees produce thousands to millions of offspring (Petit and Hampe, 2006). These characteristics allow trees to respond to selection very efficiently. However, regarding Fady & Bozzano’s example of *Pinus pinea*, recent research shows “reduced rates of adaptive evolution and a significant accumulation of genetic load” (Jaramillo-Correa et al., 2020). Thus, the importance of large Ne remains a strong rule, even for tree populations.

Defining tree populations is challenging but is often feasible. We must address two situations: fragmented and continuous forests. (1) Fragmented patches are not necessarily genetically isolated populations- they may be connected by gene flow e.g. through pollen (Fig. 1A). Forest ecologists can and do assimilate patches (sometimes without genetic data) into genetically cohesive populations; it is for these defined, larger populations that Ne should be estimated. (2) In contrast, many forests have continuous distributions and gene flow over huge areas. Delineating populations may require genetic analysis to define independent units, or use of ecosystem classifications to define a focal area. For example, foresters in British Columbia aim to ensure three populations, each with 5000 mature trees, per ecoregion (Wang et al., 2020).

Knowledge of mutation rate is not necessary. We must clarify some confusion about Ne itself. By mentioning mutation rate, we deduce that Fady & Bozzanorefer to *historic Ne* - the harmonic mean of past Ne (e.g. the coalescent Ne), which incorporates mutation rate. However, historic Ne can reflect hundreds of generations of population size changes. Our indicator focuses instead on *contemporary Ne*, which measures ongoing and near-term genetic erosion. *Contemporary Ne* is what biodiversity policy and action can change. While low historic Ne is important because it can result in low extant genetic diversity, high contemporary Ne can slow or halt further loss. Estimating contemporary Ne does not require knowing the mutation rate- instead, it requires one of the following: knowledge of demography (e.g. census size, Nc; average number of, and variance in, offspring), genetic data (to measure linkage disequilibrium, kinship or drift), or a “rule of thumb” to convert Nc to Ne, to which we now turn.

Taxon-specific thresholds are useful for Ne/Nc, but are impractical. Rules of thumb in biodiversity policy reflect trade-offs between pragmatism and specificity. Necessary and common rules include IUCN Red List thresholds, limits on sustainable harvest, and captive breeding approaches. We offered the rule of thumb Ne/Nc = 0.1 to roughly estimate contemporary Ne from Nc, in the absence of robust genetic or demographic assessments. Although Ne/Nc differs among taxa, these differences are not ‘extremely large’. Our compilation showed that most observations (roughly 63%) had Ne/Nc of 0.05 to 0.5 (Fig. 1B). All plant Ne/Nc estimates fall within 0.07 and 0.7, and 76% fall between 0.1 and 0.5. The three Ne/Nc estimates for trees fall between 0.09 and 0.3. We also note that Ne/Nc $\geq$ 0.1 is not based on the median; it is a conservative minimum threshold covering 95% of plants and 77% of species, indicating its applicability for most species. Moreover, those species for which it does not apply usually have particular characteristics, such as large variances in reproductive output or skewed sex ratio. We agree that when life history is known, conservationists should calculate (and report) Ne/Nc to amend the rule of thumb and improve our knowledge base. When Ne cannot be calculated, Nc > 5000 is a useful threshold for guiding genetic diversity conservation.

EUFORGEN indicators are a partial solution. We agree that revised Forest Europe indicators are useful, particularly the sub-indicator to maintain populations because their “adaptive genetic diversity is likely to reflect the ecological conditions in which they grow.” This aligns with our proposed CBD genetic indicator 2 (Hoban et al., 2020). Yet EUFORGEN indicators do not sufficiently address *genetic erosion or adaptive capacity within populations*, leading to our suggestion to measure and report Ne. Fady & Bozzano also propose tracking “genetic diversity measures such as heterozygosity or allelic richness” over time. We agree;

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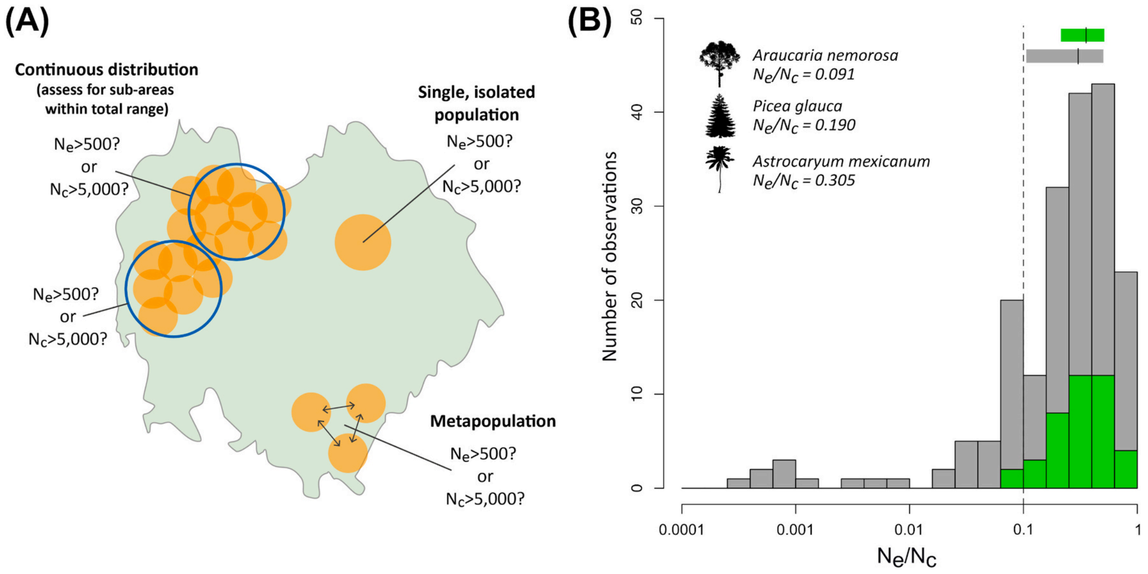

Fig. 1. Panel A: Conceptual illustration of the proposed CBD genetic diversity indicator (Laikre et al., 2020, Hoban et al., 2020) using effective population size $Ne > 500$. Ne should be assessed (using genetic or demographic techniques or a rule of thumb) for 'populations' which may include single, isolated populations; metapopulations; or sub-areas of the total range. In the absence of robust genetic or demographic assessments allowing direct estimation of Ne, we suggest to use the proxy $Ne/Nc = 0.1$ Panel B: Histogram of 214 mean Ne/Nc ratios reviewed in Hoban et al. (2020) for (i) all taxa (grey, $N = 214$) and (ii) for plants (green, $N = 41$). The dotted line indicates the threshold Ne/Nc value of 0.1 recommended in Hoban et al. (2020) in the absence of robust genetic or demographic data. Upper boxes indicate 25–75% quartiles. Ne/Nc values for available tree species shown as insert; these are in agreement with estimates from seed orchards e.g. 0.14–0.17 in *Myroxylon peruiferum*, (Silvestre et al., 2018). *Note*: the top ten and the bottom ten values from Hoban et al. (2020) were excluded for visualizing the histogram, although these values were retained for quartiles estimation. *Note*: These 214 ratios come from multiple types of Ne (demographic estimates using fluctuations in population size, reproductive output and sex ratios; temporal genetic; LD genetic; and others), and also many represent a mean of multiple populations- we acknowledge that combining them obscures this fact. We merely aim to illustrate that most estimates are near and slightly above 0.1, and that plants including trees are consistent with this pattern. Detailed examination of our data shows that subsets of each type also have medians slightly above 0.10. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this aligns with our indicator 3. We fully support monitoring of forest tree genetic diversity and conservation of local adaptation using multiple indicators.

Conclusion: We acknowledge that Ne has some limitations, including for forest trees, but we argue that $Ne > 500$ remains a suitable indicator because it is directly connected to maintaining genetic diversity for all species. Ne is possible to estimate in many cases using genetic or life history data. *In the absence of such information, the rule of thumb of $Ne/Nc = 0.1$ is an empirically justified, conservative threshold for many if not most organisms.* The $Ne > 500$ threshold and Ne/Nc rule are applicable for trees, although defining populations is challenging and requires expertise. The three indicators proposed in our paper and in Laikre et al. (2020) are simple, universal, aligned with past CBD targets, and tightly connected to genetic erosion and management of genetic diversity, thus filling an important gap in CBD indicators (Hoban et al., 2020). They are complementary and thus valuable to report in combination. Indicators 1 and 2 do not require genetic data, which is still important for most countries globally. Of course, their application in practice by national governments will still require further development and detailed guidance, which is forthcoming.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Hoban, S., Bruford, M., D'Urban Jackson, J., Lopes-Fernandes, M., Heuertz, M., Hohenlohe, P.A., Paz-Vinas, I., Sjögren-Gulve, P., Segelbacher, G., Vernesi, C., Aitken, S., Bertola, L.D., Bloomer, P., Breed, M., Rodríguez-Correa, H., Funk, W.C., Grueber, C.E., Hunter, M.E., Jaffe, R., Liggins, L., Mergeay, J., Moharrek, F., O'Brien, D., Ogden, R., Palma-Silva, C., Pierson, J., Ramakrishnan, U., Simo-Droissart, M., Tani, N., Waits, L., Laikre, L., 2020. Genetic diversity targets and indicators in the CBD post-2020 global biodiversity framework must be improved. Biol. Conserv. 248, 108654.

Jaramillo-Correa, J.P., Bagnoli, F., Grivet, D., Fady, B., Aravanopoulos, F.A., Vendramin, G.G., González-Martínez, S.C., 2020. Evolutionary rate and genetic load in an emblematic Mediterranean tree following an ancient and prolonged population collapse. Mol. Ecol. https://doi.org/10.1111/mec.15684.

Laikre, L., Hoban, S., Bruford, M.W., et al., 2020. Post-2020 goals overlook genetic diversity. Science 367 (6482), 1083–1085.

Petit, R.J., Hampe, A., 2006. Some evolutionary consequences of being a tree. Annu. Rev. Ecol. Evol. Syst. 37, 187–214.

Silva, A.R., Resende-Moreira, L.C., Carvalho, C.S., Lanes, E.C.M., Ortiz-Vera, M.P., Viana, P.L., Jaffé, R., 2020. Range-wide neutral and adaptive genetic structure of an endemic herb from Amazonian Savannas. AoB Plants 12, laa003.

Silvestre, E., de, A., Schwarcz, K.D., Grando, C., de Campos, J.B., Sujii, P.S., Tambarussi, E.V., Macrini, C.M.T., Pinheiro, J.B., Brancalion, P.H.S., Zucchi, M.I., 2018. Mating System and Effective Population Size of the Overexploited Neotropical Tree (Myroxylon peruiferum L.f.) and Their Impact on Seedling Production. J. Hered. 109, 264–271.

Wang, T., Smets, P., Chourmouzis, C., Aitken, S., Kolotelo, D., 2020. Conservation status of native tree species in British Columbia. Global Ecology and Conservation 24, e01362.

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