



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, N_e (Fady and Bozzano, 2020; 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, N_e 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) (Fady and Bozzano, 2020).

Drawing on examples for forest trees, Fady & Bozzano argue that: $N_e > 500$ is not applicable to all species because small populations are not necessarily at risk of genetic diversity loss; estimating N_e and defining populations can sometimes be difficult; and use of a general rule N_e/N_c ratio of 0.1 obscures variation among taxa. They suggest that the N_e 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.

$N_e > 500$ 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 N_e (Silva et al., 2020). Trees may tolerate low N_e 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” (Fady and Bozzano, 2020; Jaramillo-Correa et al., 2020). Thus, the importance of large N_e 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 N_e 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 N_e itself. By mentioning mutation rate, we deduce that Fady & Bozzano refer to *historic* N_e - the harmonic mean of past N_e (e.g. the coalescent N_e), which incorporates mutation rate (Fady and Bozzano, 2020). However, *historic* N_e can reflect hundreds of generations of population size changes. Our indicator focuses instead on *contemporary* N_e , which measures ongoing and near-term genetic erosion. *Contemporary* N_e is what biodiversity policy and action can change. While low *historic* N_e is important because it can result in low extant genetic diversity, high *contemporary* N_e can slow or halt further loss. Estimating *contemporary* N_e does not require knowing the mutation rate- instead, it requires one of the following: knowledge of demography (e.g. census size, N_c ; average number of, and variance in, offspring), genetic data (to measure linkage disequilibrium, kinship or drift), or a “rule of thumb” to convert N_c to N_e , to which we now turn.

Taxon-specific thresholds are useful for N_e/N_c , 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 $N_e/N_c = 0.1$ to roughly estimate *contemporary* N_e from N_c , in the absence of robust genetic or demographic assessments. Although N_e/N_c differs among taxa, these differences are not ‘extremely large’. Our compilation showed that most observations (roughly 63%) had N_e/N_c of 0.05 to 0.5 (Fig. 1B). All plant N_e/N_c estimates fall within 0.07 and 0.7, and 76% fall between 0.1 and 0.5. The three N_e/N_c estimates for trees fall between 0.09 and 0.3. We also note that $N_e/N_c \geq 0.1$ 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) N_e/N_c to amend the rule of thumb and improve our knowledge base. When N_e cannot be calculated, $N_c > 5000$ 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

<https://doi.org/10.1016/j.biocon.2020.108906>

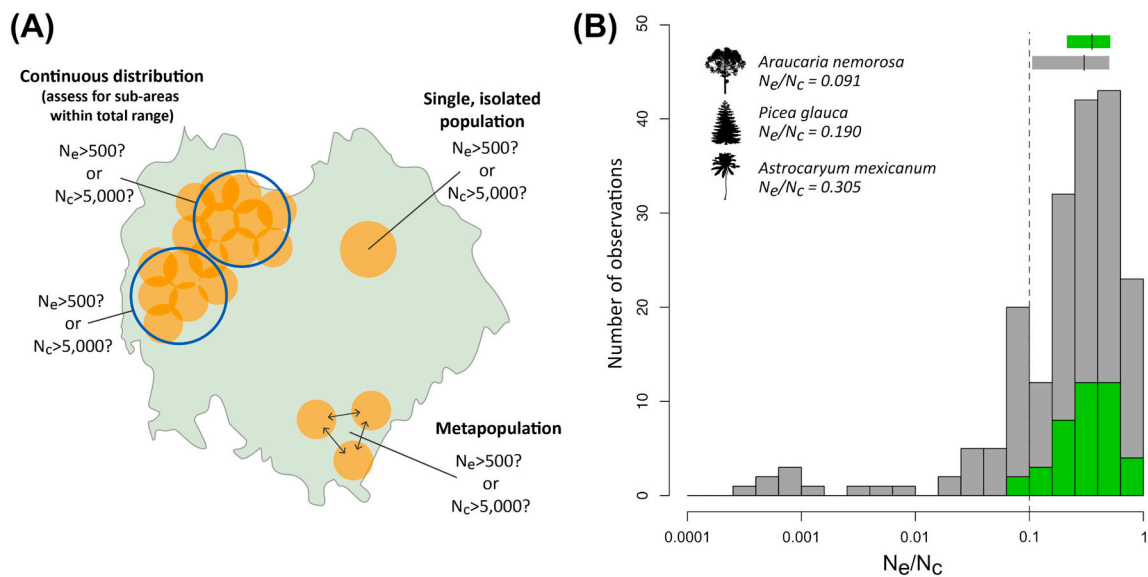


Fig. 1. Panel A: Conceptual illustration of the proposed CBD genetic diversity indicator (Laikre et al., 2020, Hoban et al., 2020) using effective population size $N_e > 500$. N_e should be assessed (using genetic or demographic techniques or a rule of thumb) for ‘populations’ which may include single, isolated populations; meta-populations; or sub-areas of the total range. In the absence of robust genetic or demographic assessments allowing direct estimation of N_e , we suggest to use the proxy $N_e/N_c = 0.1$. Panel B: Histogram of 214 mean N_e/N_c 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 N_e/N_c 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. N_e/N_c values for available tree species shown as insert; these are in agreement with estimates from seed orchards e.g. 0.14–0.17 in *Myroxyton 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 N_e (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.)

adaptive capacity within populations, leading to our suggestion to measure and report N_e . Fady & Bozzano also propose tracking “genetic diversity measures such as heterozygosity or allelic richness” over time (Fady and Bozzano, 2020). We agree; 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 N_e has some limitations, including for forest trees, but we argue that $N_e > 500$ remains a suitable indicator because it is directly connected to maintaining genetic diversity for all species. N_e is possible to estimate in many cases using genetic or life history data. *In the absence of such information, the rule of thumb of $N_e/N_c = 0.1$ is an empirically justified, conservative threshold for many if not most organisms.* The $N_e > 500$ threshold and N_e/N_c 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.

Acknowledgments

We gratefully acknowledge discussions with Richard Frankham on the types of N_e/N_c values collected in Hoban et al., 2020, and on the usefulness of the N_e/N_c ratio. Paulette Bloomer also provided helpful comments. Also, Jerker Lokrantz helped with the Figure. Funding from the Swedish Research Council Formas (FR-2016/0005, FR-2020/0008) to L.L. is acknowledged.

Disclaimer

This correspondence does not represent the official finding or policy of any government or institution but only the authors’ opinion. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government or any government.

References

- Fady, Bruno, Bozzano, Michele, 2020. Effective population size does not make a practical indicator of genetic diversity in forest trees. *Biological Conservation*, 108904. <https://doi.org/10.1016/j.biocon.2020.108904>. ISSN 0006-3207.
- 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., Oden, 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.
- Sean Hoban^{a,*}, Ivan Paz-Vinas^r, Sally Aitken^b, Laura D. Bertola^c, Martin F. Breed^d, Michael W. Bruford^e, W. Chris Funk^f, Catherine E. Grueber^g, Myriam Heuertz^h, Paul Hohenloheⁱ, Margaret E. Hunter^j, Rodolfo Jaffé^k, Margarida Lopes Fernandes^l, Joachim Mergeay^m, Farideh Moharrek^{n,o}, David O'Brien^q, Gernot Segelbacher^s, Cristiano Vernesi^t, Lisette Waits^p, Linda Laikre^{u,*}
- ^a *The Morton Arboretum, Center for Tree Science, 4100 Illinois Route 53, Lisle, IL 60532, USA*
- ^b *Forest Sciences Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada*
- ^c *City College of New York, 160 Convent Ave., New York, NY 10031, USA*
- ^d *College of Science and Engineering, Flinders University, Bedford Park, SA 5042, Australia*
- ^e *School of Bioscience, Cardiff University, Sir Martin Evans Building, Museum Avenue, UK*
- ^f *Department of Biology, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA*
- ^g *School of Life and Environmental Sciences, The University of Sydney, NSW 2006, Australia*
- ^h *Biogeco, INRAE, Univ. Bordeaux, 69 route d'Arcachon, 33610 Cestas, France*
- ⁱ *Institute for Bioinformatics and Evolutionary Studies, Department of Biological Sciences, University of Idaho, Moscow, ID 83844, USA*
- ^j *U.S. Geological Survey, Wetland and Aquatic Research Center, 7920 Northwest 71st Street, Gainesville, FL 32653, USA*
- ^k *Instituto Tecnológico Vale, Rua Boaventura da Silva #955, 66055-090 Belém, PA, Brazil*
- ^l *Instituto da Conservação da Natureza e das Florestas, IP, Lisbon, Portugal*
- ^m *Research Institute for Nature and Forest, Havenlaan 88, 1000 Brussels, Belgium*
- ⁿ *Department of Life Sciences, Natural History Museum, London SW7 5BD, UK*
- ^o *Faculty of Biological Sciences, Tarbiat Modares University, Tehran 14115-154, Iran*
- ^p *Dept Fish and Wildlife Sciences, University of Idaho, Moscow, ID, USA*
- ^q *Scottish Natural Heritage, Leachkin Road, Inverness IV3 8NW, UK*
- ^r *Laboratoire Evolution & Diversité Biologique, Centre National pour la Recherche Scientifique, Institut de Recherche pour le Développement, Université de Toulouse, UPS, CNRS, IRD, UMR 5174, 118 route de Narbonne, Toulouse 31062, France*
- ^s *Wildlife Ecology and Management, University Freiburg, Tennenbacher Str.4, D-79106 Freiburg, Germany*
- ^t *Forest Ecology and Biogeochemical Fluxes Unit, Research and Innovation Centre-Fondazione Edmund Mach, 38010 S. Michele all'Adige, TN, Italy*
- ^u *Department of Zoology, Division of Population Genetics, Stockholm University, SE10691 Stockholm, Sweden*
- * Corresponding authors.
E-mail addresses: shoban@mortonarb.org (S. Hoban), ivanpaz23@gmail.com (I. Paz-Vinas), sally.aitken@ubc.ca (S. Aitken), laura.bertola@gmail.com (L.D. Bertola), martin.breed@flinders.edu.au (M.F. Breed), brufordmw@cardiff.ac.uk (M.W. Bruford), Chris.Funk@colostate.edu (W.C. Funk), catherine.grueber@sydney.edu.au (C.E. Grueber), myriam.heuertz@inrae.fr (M. Heuertz), hohenlohe@uidaho.edu (P. Hohenlohe), mhunter@usgs.gov (M.E. Hunter), r.jaffe@ib.usp.br (R. Jaffé), margaridafernandes@icnf.pt (M.L. Fernandes), joachim.mergeay@inbo.be (J. Mergeay), farideh.moharrek@gmail.com (F. Moharrek), david.obrien@nature.scot (D. O'Brien), gernot.segelbacher@wildlife.uni-freiburg.de (G. Segelbacher), cristiano.vernesi@fmach.it (C. Vernesi), lwaits@uidaho.edu (L. Waits), linda.laikre@popgen.su.se (L. Laikre).