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Jan Perret

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Biologie des Populations et Écologie

École doctorale GAIA

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« Les plantes sont immobiles et attendent qu'on vienne les compter » :
confronter mesures in situ et simulations numériques pour améliorer
les méthodes de suivi des populations de plantes

Présentée par Jan Perret
le 14 avril 2023

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Résumé

Les suivis de population jouent un rôle central dans la conservation de la biodiversité. Ils permettent d'estimer les tailles et les tendances des populations, deux informations cruciales pour identifier les populations menacées d'extinction, comprendre les causes de leur déclin, puis tester et valider des moyens pour enrayer ce phénomène. Cependant, l'efficacité des suivis est controversée, notamment car ils souffrent de problèmes méthodologiques récurrents qui peuvent les empêcher de fournir des estimations précises et non-biaisées des tailles et des tendances de population. Cela semble être particulièrement le cas pour les populations de plantes, car les erreurs d'observation, l'une des principales sources d'erreurs des suivis de population, sont la plupart du temps ignorées. Réduire l'incertitude des estimations et s'assurer qu'elles ne sont pas biaisées permet de réduire le risque de commettre des erreurs de décision, qui peuvent mener à la mise en œuvre de mesures de conservation inefficaces voire néfastes. L'objectif de mon doctorat était d'améliorer les méthodes de suivi des populations de plantes afin qu'elles puissent fournir des estimations plus précises et non biaisées des tailles et des tendances de population. Pour cela, je me suis intéressé aux deux principaux problèmes méthodologiques des suivis de population : d'une part les plans d'échantillonnage, et d'autre part les erreurs d'observation, et plus spécifiquement la détection imparfaite. Mes travaux se sont déroulés selon trois axes.

Le premier axe a consisté à réaliser une synthèse de la littérature sur les méthodes de suivi des populations de plantes. J'ai structuré cette synthèse selon les deux principaux défis des suivis de population (l'échantillonnage et les erreurs d'observation) et les deux échelles où les suivis peuvent être réalisés (au niveau de la population et au niveau des individus). Grâce à ce travail de synthèse, j'ai identifié les sujets de recherche méthodologique prioritaires pour améliorer les suivis, et mis en lumière les différences entre les réelles lacunes de développement méthodologique et les manques de mise en œuvre de méthodes déjà existantes.

Dans le deuxième axe, j'ai utilisé des simulations numériques pour comparer la précision des estimations de taille de population obtenues avec trois méthodes d'échantillonnage différentes pour des populations dont les individus étaient plus ou moins

spatialement agrégées. L'agrégation spatiale est une caractéristique courante des populations de plantes, et cela rend les estimations de taille de population moins précises par rapport à des populations spatialement homogènes. Les simulations ont mis en évidence d'importantes différences de précision entre les méthodes d'échantillonnage, et cela m'a permis de proposer une méthode pour améliorer la précision des estimations en adaptant le plan d'échantillonnage au niveau d'agrégation de la population étudiée.

L'objectif du troisième axe était de vérifier que la détection des individus est imparfaite lorsque l'on compte des individus non marqués, ce qui n'avait pas encore été montré formellement. Pour cela, j'ai réalisé une expérimentation durant laquelle un grand nombre d'observateurs ont compté des plantes de différentes espèces dans différents habitats, et ce avec plusieurs méthodes de comptage. Les résultats ont montré que la détection des individus est imparfaite peu importe l'espèce, l'habitat et la méthode de comptage employée. De plus, cela a permis de décrire comment la probabilité de détection des individus varie selon de multiples facteurs écologiques (visibilité de l'espèce, fermeture de l'habitat, etc.) et observationnels (méthode et temps de comptage, expérience de l'observateur). Cela a également permis de donner des recommandations pour réduire la variabilité des comptages en adaptant la méthode d'observation aux conditions de l'étude.

Keywords— Biodiversité - Biologie de la Conservation - Botanique - Dynamique des populations - Evaluation de la biodiversité - Méthode d'échantillonnage

Abstract

Population monitoring programmes play a central role in biodiversity conservation. They provide estimates of population sizes and trends, which are crucial to identify populations at risk of extinction, to understand the causes of their decline, and subsequently to test and validate ways to halt this phenomenon. However, the effectiveness of monitoring programmes is controversial, because they suffer from recurrent methodological issues that may prevent them from providing precise and unbiased estimates of population sizes and trends. This seems to be particularly the case for plant populations, because observation errors, one of the main sources of error in population monitoring, are usually ignored. Reducing the uncertainty of estimates and ensuring that they are unbiased reduces the risk of making decision errors, which may result in ineffective or even harmful conservation measures. The aim of my PhD was to improve plant population monitoring methods so that they can provide more precise and unbiased estimates of population sizes and trends. To this end, I addressed the two main methodological issues of population monitoring : sampling designs and observer errors, and specifically imperfect detection. My work was conducted along three main axes.

The first axis consisted of a synthesis of the literature on plant population monitoring methods. I structured this synthesis according to the two main challenges of population monitoring (sampling and observation errors) and the two scales at which monitoring can be carried out (at the level of the population as a whole and at the level of the individuals). Thanks to this synthesis, I identified priorities for methodological research to improve monitoring programmes, and highlighted the differences existing between real gaps in methodological development and the lack of implementation of existing methods.

In the second axis, I used computer simulations to compare the precision of population size estimates obtained with three different sampling methods for populations whose individuals were more or less spatially aggregated. Spatial aggregation is a common feature of plant populations, and this makes population size estimates less precise compared to spatially homogeneous populations. The simulations highlighted substantial differences in precision between the sampling methods, and it allowed me to provide

a method to improve the precision of estimates by adapting the sampling design to the level of aggregation of the studied population.

The goal of the third axis was to verify that the detection of individuals is imperfect when counting unmarked individuals, which had not yet been formally shown. To this end, I conducted an experiment in which a large number of observers counted plants of different species, in different habitats and with three counting methods. The results showed that the detection of individuals is imperfect whatever the species, the habitat and the counting method. In addition, it allowed to describe how the detection probability of individuals varies depending on multiple ecological (species visibility, habitat closure, etc.) and observational factors (counting method, counting time and experience of the observer). It also allowed to provide recommendations to reduce the variability of counts by adapting the observation method to the study conditions.

Keywords— Biodiversity - Biodiversity assessment - Botany - Conservation biology - Population dynamics - Sampling methods

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Lis martagon (*Lilium martagon*), massif des Écrins, juin 2019.

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Pavot des Alpes (*Papaver alpinum*), massif du Taillefer, juin 2022.

Introduction générale

En 1497, un explorateur vénitien au service de l'Angleterre, Giovanni Caboto, redécouvrait une terre à l'ouest de l'Islande qui avait été découverte vers l'an 1000 par des explorateurs vikings. Il la nomma « Terre-Neuve », et aurait déclaré qu'au large de ses côtes les eaux grouillaient tellement de morues « qu'elles bloquaient l'avancée de ses bateaux » et « qu'il suffisait de plonger un panier dans l'eau pour en attraper » (BRIÈRE, 1990). Ces déclarations sont difficilement vérifiables et étaient peut-être exagérées. Toujours est-il que la pêche à la morue a été l'une des principales activités économiques de l'Est du Canada pendant quatre siècles, avec des prises augmentant progressivement jusqu'à atteindre 500 000 tonnes par an dans les années 1950. A la fin des années 1950, les techniques de pêche sélective (palangre et filet maillant) furent remplacées par la pêche au chalut. Les prises devinrent alors non sélectives et augmentèrent fortement jusqu'à atteindre 1 800 000 tonnes en 1968. Il s'ensuivit un effondrement rapide des stocks, et un arrêt de la pêche en 1992, faisant suite à plusieurs tentatives infructueuses de limitation des prélèvements (HAMILTON et al., 2004). En 2021, les stocks de morues étaient encore loin des niveaux historiques malgré presque 30 ans d'arrêt de la pêche, et il n'est pas certain qu'ils retrouvent ces niveaux un jour (MPO, 2021). Les principales causes de l'effondrement spectaculaire des populations de morue de Terre-Neuve sont la surexploitation rendue possible par les techniques de pêche industrielle et les forts enjeux socio-économiques associés. En plus de cela, les stocks de morue ont été surestimés plusieurs fois à cause d'une méthode d'estimation inadaptée et le fonctionnement des populations était mal compris, ce qui a empêché de mettre en place à temps des politiques de conservation efficaces (WALTERS & MAGUIRE, 1996).

En 1962, la biologiste américaine Rachel Carson publiait le livre *Silent Spring* (CARSON, 1962). Elle y exposait les dangers pour l'environnement et la santé humaine des pesticides chimiques, en particulier du DDT, un insecticide. Elle y décrivait en particulier les effets dévastateurs de ces produits sur les oiseaux, chez qui l'exposition au DDT occasionne une hausse de la mortalité et des problèmes de reproduction, d'où le titre du livre, qui préfigurait ce qui aurait pu arriver si le DDT avait continué à être utilisé. Le livre a fait l'objet d'une campagne de dénigrement orchestrée par l'industrie chimique américaine, mais cela n'a pas empêché la tenue d'un vaste débat public, débouchant sur l'adoption de plusieurs lois réglementant l'usage des pesticides et interdisant le DDT aux Etats-Unis en 1972 (DUNN, 2012). Suite à cette interdiction et

à d'autres mesures de protection concomitantes comme l'Endangered Species Act de 1973, plusieurs espèces d'oiseaux qui étaient en danger critique d'extinction aux États-Unis dans les années 1960 ont vu leurs populations se rétablir progressivement, dont la plus emblématique est le Pygargue à tête blanche (*Haliaeetus leucocephalus*; GRIER, 1982).

En 2017 paraissait un article estimant que la biomasse d'insectes volants avait chuté de 76% entre 1989 et 2016 dans un réseau de réserves naturelles allemandes (HALLMANN et al., 2017). Cette étude a été fortement médiatisée en Europe, probablement grâce à sa grande étendue spatiale et temporelle, ainsi qu'à ses résultats alarmants et faciles à communiquer. En outre, le fait qu'elle portait sur des réserves naturelles a certainement renforcé la médiatisation du message, puisque l'impact direct des activités humaines sur l'environnement y est a priori limité. D'autres études ont rendu compte de déclin importants de la quantité d'insectes, mais elles sont inégalement réparties dans le monde et ne portent pas toutes sur les mêmes périodes ni les mêmes taxons, ce qui rend difficile de mesurer l'ampleur de ce phénomène à l'échelle mondiale (RHODES, 2018; WAGNER, 2020). Les principales causes du déclin des insectes en Europe sont l'intensification de l'agriculture, le changement d'utilisation des sols et les insecticides agricoles, mais les déclins observés dans d'autres régions du monde pourraient être principalement causés par le changement climatique (e.g. LISTER & GARCIA, 2018). En Europe, de nombreuses personnes ont pu noter empiriquement ce déclin des insectes lors de trajets régulièrement parcourus en voiture, durant lesquels de moins en moins d'insectes s'écrasaient sur les pare-brises au fil des années. Cela a été appelé le « *windshield effect* » dans la littérature scientifique, et il a été montré que la quantité d'insectes s'écrasant sur les pare brises donnait des résultats similaires à d'autres méthodes de mesure de la quantité d'insectes volants (MØLLER, 2019).

0.1 La biodiversité en crise

Une crise d'extinction massive, ou crise de la biodiversité, est un événement relativement bref à l'échelle des temps géologiques durant lequel on estime qu'au moins 75% des espèces vivantes de macro-organismes se sont éteintes. Au début de l'Holocène (12 000 ans avant le présent), la biosphère est entrée dans sa **sixième crise d'extinction**

massive, et les extinctions s'accélérent depuis le début du 19^{ème} siècle (BARNOSKY et al., 2011 ; PIMM et al., 2014). Contrairement aux crises précédentes, cette sixième crise est causée principalement par les actions de l'espèce humaine (IPBES, 2019). J'ai choisi de présenter les trois exemples en exergue de ce manuscrit car ce sont des illustrations de cette crise qui m'ont particulièrement marqué au cours de mes études universitaires. Il s'agit également d'un exemple d'échec de protection de la biodiversité, d'un exemple de réussite, et d'un exemple de crise en cours dont l'issue est incertaine. L'effondrement des populations de morues du Nord-Ouest de l'Atlantique est une **tragédie des biens communs** (au sens de HARDIN, 1968), durant laquelle les intérêts socio-économiques liés à la pêche et une évaluation trop incertaine de l'état des populations ont mené à l'épuisement presque total des populations. Le livre *Silent Spring* de Rachel Carson montre qu'une bonne compréhension des causes de problèmes environnementaux et la publication de ces informations peuvent permettre d'éviter des extinctions d'espèces et de graves problèmes de santé publique, malgré la présence de puissants intérêts économiques. Le déclin des insectes est exceptionnel car il a été tellement fulgurant en Europe de l'Ouest que de nombreuses personnes ont pu l'observer à leur échelle, alors que les manifestations de la crise de la biodiversité échappent généralement à notre observation directe (SOGA & GASTON, 2018). En effet, ces modifications de notre environnement ont souvent lieu sur de trop longues échelles de temps pour que nous puissions nous en rendre compte, ou du moins pour que nous soyons sûrs que quelque chose a changé. On parle d'**amnésie écologique** (en anglais *shifting baseline syndrome*), c'est-à-dire que chaque personne prend comme état de référence d'un écosystème celui qu'elle a connu durant sa jeunesse, et ne remarque pas si l'écosystème se dégrade lentement. Avec la succession des générations, des dégradations très importantes mais progressives peuvent ainsi passer inaperçues (PAULY, 1995). Ces modifications de notre environnement concernent aussi souvent des espèces ou des espaces difficiles à observer, pour lesquels seulement une partie de la société peut remarquer des changements, comme par exemple les pêcheurs de morues de Terre-Neuve ou les ornithologues étudiant la reproduction du Pygargue à tête blanche en Amérique du Nord. Cela est d'autant plus vrai que les humains vivent de plus en plus en ville et sont de plus en plus déconnectés de la nature (CAZALIS et al., 2023).

La crise de la biodiversité se traduit notamment par une **réduction d'abondance**

de nombreuses populations d'espèces animales et végétales, pouvant aller jusqu'à l'extinction de certaines populations. Une des évaluations les plus globales de ce phénomène est l'Indice Planète Vivante, qui a permis d'estimer que l'abondance des populations de vertébrés avait en moyenne diminué de 69% entre 1970 et 2018 (WWF, 2020). Cependant, les données disponibles font que les populations d'oiseaux et les espèces des régions tempérées sont surreprésentées dans le calcul de cet indice, qui est donc moins représentatif pour les autres taxons et les régions tropicales (COLLEN et al., 2009). La crise de la biodiversité se traduit aussi par une vitesse d'**extinction des espèces** plusieurs centaines de fois supérieure à la vitesse d'extinction "normale", c'est-à-dire en dehors des précédentes crises d'extinctions massives (PIMM et al., 2014). L'objectif de la liste rouge des espèces menacées d'extinction de l'Union Internationale pour la Conservation de la Nature (abrégé « IUCN » selon l'appellation anglaise) est de fournir une estimation régulièrement mise à jour du niveau de risque d'extinction pour le plus grand nombre d'espèces possibles. En 2022, l'IUCN estimait ainsi que 28% des espèces de plantes et d'animaux pour lesquelles elle avait pu estimer ce risque avaient un risque élevé de s'éteindre d'ici 100 ans (IUCN, 2022). Si l'on décompose ce taux par taxon, 41% des espèces d'amphibiens, 27% des espèces de mammifères, 21% des espèces de reptiles et 16% des espèces d'odonates étaient par exemple jugées menacées d'extinction. Les plantes n'échappent pas au phénomène, puisque l'IUCN estime que sur une sélection d'espèces de dicotylédones, 39% sont menacées, et que c'est également le cas de 34% des espèces de conifères du monde. Pour les vertébrés terrestres, si toutes les espèces actuellement jugées menacées par l'IUCN s'éteignent d'ici un siècle et que la vitesse d'extinction reste constante, le seuil des 75% d'espèces éteintes sera atteint d'ici 240 à 540 ans, ce qui ferait de la crise actuelle la plus rapide que la biosphère ait connue (BARNOSKY et al., 2011).

Durant la préhistoire, les extinctions d'espèces étaient principalement causées par la surchasse (notamment pour la mégafaune, voir SANDOM et al., 2014) et la modification des habitats naturels liée à l'installation des communautés humaines sur de nouveaux territoires (BAYON et al., 2012). Le changement climatique ayant eu lieu à la fin de la dernière ère glaciaire a également pu jouer un rôle, bien qu'il ait a priori été secondaire (KOCH & BARNOSKY, 2006). Actuellement, **cinq causes principales** sont à l'origine des risques d'extinction des espèces, et toutes sont d'origine anthro-

gique (HOGUE & BREON, 2022). La première cause est la **destruction des habitats** des espèces par les activités humaines, qui est une menace pour 88% des espèces actuellement jugées menacées d'extinction. La destruction des habitats est principalement due à l'expansion et l'intensification de l'agriculture, la déforestation et l'urbanisation. Il s'agit par exemple de la principale cause d'extinction de populations d'espèces de plantes rares en zone méditerranéenne française au cours du dernier siècle (LAVERGNE et al., 2005). La deuxième cause d'extinction des espèces est la **surexploitation** des ressources naturelles, comme dans le cas de la pêche ou de la cueillette, qui entre en jeu pour 27% des espèces menacées. Les trois menaces suivantes par ordre d'importance sont les **espèces invasives** qui sont un facteur de risque pour 25% des espèces menacées, la **pollution** (18% des espèces menacées), et le **changement climatique** (17% des espèces menacées). L'ordre d'importance de ces menaces est voué à évoluer, et le changement climatique va certainement devenir de plus en plus prépondérant (IPBES, 2019).

Le déclin d'abondance des populations, la disparition de certaines populations et l'extinction d'espèces peuvent avoir des **conséquences importantes sur le fonctionnement des écosystèmes** (IPBES, 2019). Par exemple, la disparition d'une espèce de pollinisateur peut affecter la reproduction d'espèces de plantes qui en dépendent pour leur pollinisation, et affecter indirectement les animaux qui se nourrissent de ces plantes. Ainsi, la disparition d'une seule espèce peut suffire à perturber le fonctionnement d'un écosystème et avoir des conséquences imprévues et potentiellement importantes sur l'ensemble de l'écosystème (voir par exemple RIPPLE & BESCHTA, 2012; WATSON & ESTES, 2011). Même sans extinction de population ou d'espèce, ces modifications en cascade peuvent avoir lieu à cause du déclin d'abondance des populations. Le déclin des insectes est emblématique pour cela, puisque 87% des espèces de plantes à fleurs nécessitent une pollinisation animale, qui est assurée majoritairement par les insectes (OLLERTON et al., 2011). Le déclin des populations d'insectes peut donc entraîner une perte progressive de la fonction de pollinisation, ce qui est déjà observé dans de multiples écosystèmes et biomes, ainsi que sur des cultures agricoles (RHODES, 2018). Au travers de ces pertes de fonctions des écosystèmes, la crise de la biodiversité a des conséquences sur les populations humaines, puisqu'elles dépendent de leur environnement pour leur subsistance et leur économie. Cette dépendance a été formalisée dans la

notion de « **services écosystémiques** », c'est-à-dire les services que les communautés humaines tirent des écosystèmes. Les écosystèmes jouent notamment un rôle central dans la régulation du climat, la purification de l'air et de l'eau, la pollinisation des cultures, la régulation des maladies et des ravageurs, et la fourniture de nourriture et de matières premières comme le bois (REID, 2005). En 2019, la *Food and Agriculture Organisation* (FAO), qui dépend de l'Organisation des Nations Unies, a ainsi déclaré que le déclin de la biodiversité met en péril l'avenir de l'alimentation et de la santé de l'humanité (FAO, 2019). Enrayer le déclin de la biodiversité n'est donc pas seulement une fin en soi, mais également un enjeu économique et social, puisque c'est essentiel pour le maintien des services écosystémiques et ainsi pour notre bien-être et le fonctionnement de nos systèmes économiques.

Des formes de **protection de la nature** peuvent être trouvées dès l'Antiquité, avec la protection d'espaces naturels pour des raisons esthétiques, culturelles ou religieuses (SHER & PRIMACK, 2019). Cependant, la protection de la nature s'est réellement formalisée à la fin du 19^{ème} siècle suite à de multiples prises de conscience des conséquences des activités humaines sur les écosystèmes (voir par exemple HORNADAY, 1889). Cela a notamment mené à la création des premiers parcs nationaux aux États-Unis, le premier étant celui de Yellowstone en 1872. Par la suite, la conscience croissante que la nature n'est pas inépuisable et qu'il est nécessaire de la protéger des actions de l'Homme a donné naissance aux premières grandes organisations non gouvernementales (IUCN en 1948, WWF en 1961) et aux premiers programmes internationaux (programme "*Man and Biosphere*" de l'UNESCO en 1971) dédiés à la protection de la nature. Une étape cruciale de l'histoire de la protection de la nature a eu lieu en 1992 au Sommet de la Terre de Rio de Janeiro, où la "**Convention sur la Diversité Biologique**" a été ratifiée par 168 pays. Il s'agit de la première reconnaissance dans le droit international que la conservation de la biodiversité "est une préoccupation commune à l'humanité" et que "les Etats sont responsables de la conservation de leur diversité biologique et de l'utilisation durable de leurs ressources biologiques" (NATIONS UNIES, 1992). Depuis le sommet de Rio, les pays signataires se réunissent tous les deux ans environ lors des *Conferences of the Parties* (COP) pour faire évoluer le texte initial, la dernière étant la COP15 qui a eu lieu en décembre 2022 à Montréal au Canada. De la ratification de ces traités émergent ensuite des **politiques publiques nationales et internationales**

de protection de la nature. Par exemple, le réseau européen Natura 2000 et la stratégie nationale pour la biodiversité française sont des dispositifs initiés notamment pour atteindre les objectifs fixés par la Convention sur la Diversité Biologique (MTE, 2022 ; POPESCU et al., 2014). Pour mener à bien les politiques de protection de la nature différents **outils réglementaires** peuvent être utilisés, comme protéger des espaces naturels (c'est-à-dire réglementer l'accès et les activités qui pourront y être entreprises), protéger des espèces (c'est-à-dire réglementer des actions pouvant nuire à ces espèces) et réglementer des activités ou l'utilisation de certaines substances (par exemple l'interdiction du DDT). En plus des mesures réglementaires, des **actions sur les écosystèmes** peuvent être mises en œuvre, comme des mesures de gestion pour rendre un habitat plus favorable à une espèce, ou des renforcements de populations (HUNTER & GIBBS, 2006).

Lutter contre le déclin de la biodiversité nécessite trois éléments : (1) **identifier les espèces ou populations menacées**, (2) **comprendre les causes** de cette menace, et (3) **agir pour réduire, éliminer ou compenser ces menaces** (BARBAULT, 1997). Cependant les écosystèmes sont des systèmes complexes, et les mécanismes sous-jacents aux dynamiques des populations sont souvent difficiles à comprendre. De plus, les menaces pesant sur les populations sont souvent multiples, et peuvent avoir des relations non linéaires avec les tendances des populations. Par exemple, une population de plantes peut suivre un déclin linéaire à cause de la fragmentation de son habitat jusqu'à un certain seuil, puis connaître un brusque effondrement à cause d'une perte trop importante de diversité allélique, de la stochasticité démographique ou du manque de pollen lorsque la population passe sous une certaine densité d'individus (aussi appelé "effet Allee", voir COURCHAMP et al., 1999 ; FISCHER & MATTHIES, 1998). Il est donc fréquent qu'il y ait de l'incertitude sur les niveaux de menace pesant sur les populations et que les causes sous-jacentes ne soient pas parfaitement comprises. Lutter contre la crise de la biodiversité nécessite néanmoins de **prendre des décisions malgré ces incertitudes**, comme choisir quelles espèces et populations protéger en priorité et quelles actions mettre en œuvre (SOULÉ, 1985).

0.2 Démographie et statistiques au service de la biologie de la conservation

En parallèle de la prise de conscience politique quant à la nécessité de protéger la nature, une nouvelle discipline scientifique a vu le jour au cours du 20^{ème} siècle : la **Biologie de la Conservation**. Ses grands principes sont formalisés en 1985 par Michael Soulé dans un article intitulé “*What is Conservation Biology?*”. La biologie de la conservation y est définie comme une discipline qui “s’intéresse à la biologie des espèces, communautés et écosystèmes perturbés, directement ou indirectement, par les activités humaines ou d’autres agents”, et dont l’objectif est de “fournir des principes et outils pour préserver la diversité biologique”. Présenté d’une autre manière, les objectifs de la biologie de la conservation sont d’identifier les espèces et populations en déclin, de déterminer les causes de leur déclin, et de tester et valider des moyens pour les enrayer (BARBAULT, 1997). Un autre principe important de la biologie de la conservation est posé par Michael Soulé dans son article fondateur : il s’agit d’une **discipline de gestion de crise**, comme l’est parfois la chirurgie en médecine, où il est souvent nécessaire d’agir avant de comprendre parfaitement une situation. Limiter cette incertitude est crucial en conservation, car mieux une situation est comprise, plus les actions entreprises ont de chances de fonctionner (BURGMAN, 2005). Par ailleurs, afin de comprendre les causes et les conséquences du déclin de la biodiversité et de développer des solutions pour l’enrayer, la biologie de la conservation est le cadre de nombreux travaux interdisciplinaires entre des disciplines telles que l’écologie, la démographie et des sciences humaines et sociales telle que l’économie (PRIMACK et al., 2012).

Mes travaux de doctorat s’inscrivent dans cette discipline de la biologie de la conservation. Plus spécifiquement, je me suis concentré sur l’**étude des populations** car ce niveau écologique est beaucoup mobilisé dans les politiques publiques de conservation de la biodiversité. Par exemple, l’Indice Planète Vivante et de la liste rouge de l’IUCN sont deux indicateurs globaux du déclin de la biodiversité qui jouent un rôle important de sensibilisation du grand public et des décideurs politiques. Tous deux sont basés principalement sur des critères d’état et de dynamique de populations (IUCN, 2019; WWF, 2020). La protection d’espèces au niveau réglementaire se base également sur

une logique de population, et la création d'espaces naturels protégés est souvent motivée notamment par la volonté de protéger des populations d'espèces menacées occupant ces espaces (voir par exemple GASTON et al., 2008 ; GODET et al., 2007). Puisque j'ai choisi de travailler au niveau des populations, mes travaux s'inscrivent également dans la discipline scientifique de la démographie, en plus de la biologie de la conservation.

La **démographie** est la discipline scientifique étudiant les dynamiques temporelles et spatiales des populations humaines, animales et végétales, notamment via l'étude de la fécondité, de la survie et des migrations des individus. La démographie moderne est née au 18ème siècle avec la publication d'études sur les populations humaines de pays européens et des Etats-Unis, dont l'objectif était de prévoir les futures évolutions des populations et leurs besoins en ressources et services publics (voir par exemple FRANKLIN, 1755 ; MALTHUS, 1798). Depuis lors, la démographie a joué un rôle crucial dans l'**information des décisions de l'État**, en fournissant des renseignements sur l'état et le fonctionnement des populations (SCHELL et al., 2007). Les premières études démographiques sur des populations animales ont été menées au cours du 20ème siècle (voir par exemple LINCOLN, 1930), suivies des premières études sur des populations végétales (HARPER & WHITE, 1974). Les objectifs de ces premières études étaient principalement de mieux gérer les prélèvements de populations pêchées ou chassées. Par la suite, des études sur des populations non exploitées sont apparues, dont l'objectif était de comprendre comment protéger ces populations dans le contexte du déclin de la biodiversité (voir par exemple GRIER, 1982).

Durant mon doctorat, je me suis intéressé à l'**étude des populations de plantes**. L'approche démographique dans l'étude des populations de plantes, c'est-à-dire en mesurant quantitativement les changements de taille de population et les processus démographiques sous-jacents (taux de survie, de fécondité, etc.), a débuté une cinquantaine d'années après les premières études démographiques sur les animaux (HARPER & WHITE, 1974). Ainsi, en 1974, John Harper écrivait "L'étude de la démographie végétale n'a jamais pris un élan significatif au sein de la science de l'écologie ; les écologues des plantes se sont concentrés sur la physiologie, la structure et la taxonomie des végétations, tout en ignorant largement le phénomène des populations qui constitue le flux sous-jacent" (HARPER & WHITE, 1974). En effet, avant les années 60, les

études menées en écologie végétale étaient majoritairement descriptives et s'intéressaient à la composition des communautés, autour de concepts tels que les successions de végétations, le climax et la phytosociologie (OGDEN, 1985). Les informations sur le fonctionnement des populations de plantes venaient alors principalement d'études faites en agronomie et en foresterie, qui étaient centrées sur les questions de production de nourriture ou de bois, et pour lesquelles comprendre le fonctionnement des populations était secondaire (HARPER & WHITE, 1974; OGDEN, 1985). Les premières études à visée principalement démographique datent de la fin du 19^{ème} siècle et du début du 20^{ème} siècle (CRAWLEY et al., 1990; HARPER, 1977), mais ce sont **John Harper et ses collaborateurs** à la *School of Plant Biology (University College of North Wales)* qui ont réellement initié l'étude démographique des populations de plantes au cours des années 1960 et 1970 (OGDEN, 1985). Ils ont notamment publié une série d'articles pionniers qui ont posé les bases de l'étude démographique des populations de plantes (HARPER, 1967; HARPER & WHITE, 1974; HARPER et al., 1965; HARPER, 1964; SARUKHAN & HARPER, 1973). Parmi ces bases conceptuelles et méthodologiques, on peut citer l'adoption d'une **approche quantitative** plutôt que qualitative, de **suivre le devenir d'individus** plutôt que d'étudier la population dans son ensemble, et de chercher à **comprendre les mécanismes démographiques** plutôt que d'avoir une approche descriptive. En outre, ils ont popularisé l'utilisation de **modèles mathématiques** pour décrire le fonctionnement des populations comme cela était fait pour les populations humaines et animales, et l'**utilisation d'expériences** pour comprendre les processus démographiques. Ces décennies de recherche ont été synthétisées dans le livre *Population Biology of Plants* (HARPER, 1977), qui a pendant longtemps été une référence dans le domaine. Suite aux travaux de John Harper et de ses collaborateurs, de plus en plus d'études se sont intéressées à la dynamique des populations de plantes et aux processus démographiques sous-jacents.

Que la population étudiée soit humaine, animale ou végétale, la démographie a recours à de nombreux outils issus des **statistiques** pour analyser les données collectées et en tirer des conclusions. Mes travaux s'inscrivent donc également dans cette 3^{ème} discipline. Les statistiques sont une branche des mathématiques qui concerne la collecte, l'organisation, l'analyse et l'interprétation de données (UPTON & COOK, 2008). L'objectif principal des statistiques est de décrire et de comprendre des systèmes consti-

tués d'un grand nombre d'individus ou d'unités (DAGNELIE, 1982). Dans leur forme la plus simple, les statistiques sont nées durant l'Antiquité, puisque des recensements de bétail figurent parmi les plus anciens documents écrits ayant été retrouvés (PARKER, 1950). Pendant longtemps, les statistiques se sont résumées à la collecte d'informations par les États sur leur population, le commerce et les ressources naturelles. L'étymologie du mot « statistique » vient d'ailleurs du latin « status », qui signifie « état », car les statistiques étaient initialement la « **science de l'État** » (BALL, 2004). La naissance des statistiques modernes est généralement placée au 17^{ème} ou au 18^{ème} siècle, avec les premières études démographiques nationales mentionnées précédemment (voir par exemple GRAUNT, 1662). Les mathématiciens tels que Laplace, Gauss et Quetelet s'appuyèrent ensuite sur la théorie des probabilités pour développer les **statistiques inférentielles**. Il s'agit des méthodes permettant de déduire les caractéristiques d'un groupe d'unités, appelé la population, à partir de celles observées sur un sous-groupe de plus petite taille, appelé l'échantillon, et de fournir une mesure de l'incertitude associée à cette déduction (COCHRAN, 1977). Le procédé de sélection d'un sous-ensemble de la population est appelé "l'échantillonnage", et on parle "d'estimation statistique" et de "**mesure d'incertitude** d'une estimation" pour désigner le procédé de déduction des caractéristiques de la population à partir des observations faites sur l'échantillon. Aujourd'hui les statistiques sont utilisées dans un très grand nombre de domaines scientifiques et industriels, et jouent un rôle essentiel dans l'information des décisions des États (REY, 2016). Comme pour beaucoup d'autres disciplines scientifiques basées sur l'observation et l'expérimentation, les statistiques sont centrales en écologie et en biologie de la conservation, car les systèmes étudiés sont généralement constitués d'un trop grand nombre d'unités pour que toutes puissent être observées, ce qui rend nécessaire de recourir à l'échantillonnage (GIMENEZ et al., 2014).

La biologie de la conservation est plus jeune que la démographie et les statistiques, et a beaucoup bénéficié des méthodes développées dans ces deux disciplines (SIMBERLOFF, 1988; SOULÉ, 1985). En effet, afin d'atteindre ses objectifs, la biologie de la conservation nécessite de comprendre le fonctionnement des populations animales et végétales. La démographie et les statistiques fournissent des outils indispensables pour cela. Durant mon doctorat, je me suis intéressé aux méthodes permettant d'estimer la taille des populations de plantes à un instant donné, et aux méthodes permettant

de mesurer leurs dynamiques sur de longues échelles temporelles, comme plusieurs années ou décennies. On parle de “**tendance de population**” pour désigner la dynamique à moyen-long terme d’une population (par exemple le taux d’accroissement ou de déclin du nombre d’individus sur 10 ou 20 ans), et de “**suivi de population**” pour désigner le processus de collecte des observations qui permettront d’estimer la tendance d’une population. Les **méthodes de suivi** comprennent plusieurs aspects relatifs à la collecte d’observations ainsi qu’à leur traitement (WILLIAMS et al., 2002) : l’**échantillonnage dans l’espace et le temps** (autrement dit où et quand les observations sont réalisées), le **type de mesure** prise (par exemple des comptages d’individus ou des mesures de taux de recouvrement), la **méthode de mesure** employée (par exemple estimer visuellement le nombre d’individus en 30 secondes ou au contraire faire un comptage détaillé en temps illimité), et la **méthode statistique** utilisée pour estimer la tendance de population (par exemple un modèle de N-mixture en population ouverte ou un modèle linéaire généralisé avec distribution de Poisson).

Malgré l’importance des suivis de population pour la conservation de la biodiversité, leur **efficacité est controversée** dans la littérature scientifique (NICHOLS & WILLIAMS, 2006). Certains auteurs ont notamment affirmé que de nombreux programmes de suivi sont inefficaces, qu’ils atteignent rarement leurs objectifs de départ, et qu’ils gaspillent les ressources allouées à la conservation de la biodiversité (ANDERSON, 2001 ; LINDENMAYER & LIKENS, 2009). La majorité des critiques ne concernent pas le principe même de suivre des populations (voir cependant MCDONALD-MADDEN et al., 2010), mais la manière dont les programmes de suivis sont conçus et les méthodes qu’ils emploient. Parmi les critiques les plus fréquentes, il est remarqué que de nombreux programmes de suivi n’ont **pas d’objectifs précis** et sont par conséquent mal conçus (NICHOLS & WILLIAMS, 2006). Par exemple, ils peuvent être **sous-dimensionnés** par rapport à leurs objectifs (LEGG & NAGY, 2006), ou mesurer un très grand nombre de variables afin de répondre à une multitude d’objectifs, ce qui se fait au détriment de la qualité des données récoltées (LINDENMAYER & LIKENS, 2009). Outre ces problèmes relatifs à leurs objectifs, des **problèmes méthodologiques récurrents** empêchent de nombreux programmes de suivi de fournir des estimations précises et non biaisées des tendances (YOCCOZ et al., 2001). En statistiques, la **précision** désigne la proximité moyenne entre des estimations répétées du même paramètre, et le **biais**

désigne l'écart moyen entre de telles estimations et la valeur réelle du paramètre recherché. Autrement dit, la précision est une mesure de la dispersion des estimations (on parle aussi de mesure d'incertitude), et le biais est une mesure de l'erreur systématique des estimations. Ces deux caractéristiques sont indépendantes : des estimations peuvent être précises, non biaisées, les deux à la fois, ou au contraire à la fois imprécises et biaisées. Si un programme de suivi fournit une estimation de tendance trop imprécise il est possible que celle-ci ne soit d'aucune utilité pour prendre une décision de conservation, et si l'estimation est biaisée cela risque de déclencher des mesures inadéquates (voir par exemple GRAND et al., 2007). Même pour un programme de suivi ayant des objectifs clairs, concevoir un protocole et choisir un dimensionnement qui permettront d'obtenir des estimations non biaisées et suffisamment précises, tout en ayant le coût le plus faible possible, est une tâche complexe qui nécessite de maîtriser un certain nombre d'outils statistiques.

0.3 Le rôle central des méthodes dans les sciences naturelles

D'un point de vue épistémologique, les disciplines scientifiques peuvent être divisées en trois grandes catégories : les sciences formelles (dites aussi « sciences exactes ») telles que les mathématiques et l'informatique, les sciences naturelles telles que la démographie et la biologie de la conservation, et les sciences humaines et sociales comme par exemple l'anthropologie. Dans les sciences naturelles, les connaissances sont produites par raisonnement inductif, c'est-à-dire que des phénomènes sont observés et des lois générales sont proposées pour expliquer ces phénomènes (COPI et al., 2006). Pour pleinement comprendre l'importance des méthodes dans les sciences naturelles, il est nécessaire de comprendre le déroulement de la démarche scientifique et le rôle qu'y jouent les expérimentations et les études observationnelles. La **démarche scientifique**, aussi appelée « méthode scientifique », est une méthode empirique qui permet d'acquérir des connaissances sur le fonctionnement du monde. Elle peut être résumée aux étapes suivantes (SELLS et al., 2018) :

1. Définir une question sur le fonctionnement du monde

2. Collecter des informations sur le sujet
3. Formuler une hypothèse (ou de préférence plusieurs hypothèses alternatives, voir l'article *Strong inference* de PLATT, 1964)
4. Concevoir et réaliser une expérimentation permettant de tester la ou les hypothèse(s)
5. Analyser les données produites lors de l'expérimentation
6. Interpréter les résultats et conclure s'il faut rejeter l'hypothèse ou non
7. Publier les résultats
8. Attendre la confirmation des résultats par d'autres chercheurs qui auront reproduit indépendamment les étapes 4 à 7

Cette formulation de la démarche scientifique a souvent été critiquée comme étant simpliste et ne reflétant pas la manière dont les chercheurs travaillent au quotidien (pour un résumé de ces controverses, voir GAUCH, 2002, p.3). Comme de nombreux chercheurs, je pense qu'il faut voir cette formulation de la démarche scientifique comme un principe général à utiliser avec intelligence et créativité, et non comme une série rigide d'étapes à suivre en toutes circonstances (EINSTEIN & INFELD, 1966; GAUCH, 2002). En outre, comme l'ont montré les travaux de l'historien des sciences Thomas Kuhn, la recherche scientifique est un phénomène social. Il arrive notamment que des théories mettent longtemps à être abandonnées alors que de nombreux résultats expérimentaux les contredisent, et c'est parfois davantage le changement de génération de chercheurs que l'accumulation de preuves qui amène l'adoption de nouvelles théories (KUHN, 1962). Toujours est-il que les **expériences** sont essentielles, puisqu'il s'agit de l'étape de la démarche scientifique où a lieu l'observation du monde.

Une expérience peut être définie comme « une étude durant laquelle une intervention est délibérément réalisée pour observer ses effets » (SHADISH et al., 2001). Cette définition est très large, et il existe en réalité plusieurs types d'expériences ayant chacune des problèmes méthodologiques spécifiques. Le type d'expérience qui est considéré comme le *gold standard* est l'**expérience contrôlée**. Dans une expérience contrôlée, un système est parfaitement isolé du reste du monde et une intervention est réalisée sur ce système. Ainsi, tout changement observé du système est nécessairement la conséquence de l'intervention (DINARDO, 2008). Ce type d'expériences peut être trouvé en

physique, où il est par exemple possible d'isoler une particule dans une enceinte de confinement, mais dans beaucoup de cas il est impossible d'isoler son objet d'étude. Il est alors possible de réaliser une **expérience randomisée**, c'est-à-dire qu'une population de départ est divisée aléatoirement en deux groupes, l'un sur lequel une intervention est réalisée et l'autre sur lequel rien n'est fait, le « groupe contrôle » (FISHER, 1935). Aucun des groupes n'est isolé, mais il est possible de conclure sur les effets de l'intervention (l'**inférence causale**), car si une différence entre les deux groupes est apparue, elle est nécessairement la conséquence de l'intervention. En effet, la création aléatoire des groupes assure qu'ils sont en moyenne identiques au départ et qu'ils sont soumis aux mêmes influences extérieures durant l'expérience, hormis l'intervention réalisée (SHADISH et al., 2001). Les expériences randomisées sont parfois utilisées en biologie de la conservation pour mesurer l'effet d'une intervention de conservation, mais elles restent encore relativement rares (voir PYNEGAR et al., 2021, pour une synthèse sur les expériences randomisées en conservation et les raisons de leur actuelle rareté). Lorsqu'il n'est pas possible de réaliser une expérience randomisée, par exemple car les interventions ne peuvent pas être planifiées par l'expérimentateur, il est parfois possible de réaliser ce que l'on appelle une **quasi-expérience**. Dans une quasi-expérience, il y a bien une intervention sur un groupe d'individus et un groupe sans intervention, mais l'assignation des individus aux groupes n'est pas aléatoire et généralement pas faite par l'expérimentateur (CAMPBELL & STANLEY, 1963; REICHARDT, 2019; SHADISH et al., 2001). C'est par exemple le cas des protocoles “*Before-After Control Impact*” (BACI) utilisés en biologie de la conservation pour mesurer l'impact d'une perturbation sur un système (GREEN, 1979; SMOKOROWSKI & RANDALL, 2017). L'un des problèmes principaux des quasi-expériences est qu'elles peuvent mener à de fausses conclusions du fait de l'existence de **facteurs confondants** (FERRARO & HANAUER, 2014). Cela est d'autant plus le cas en biologie de la conservation où il est souvent difficile de contrôler les variables potentiellement confondantes. Finalement, il est parfois impossible de manipuler le système étudié, que cela soit pour des raisons éthiques (par exemple si l'espèce étudiée est menacée), ou que la question posée ne puisse pas être étudiée avec une manipulation du système. Ceci est le cas pour les suivis de populations, où l'objectif principal est d'estimer la tendance d'une population in situ. Il faut alors avoir recours à des **études observationnelles**, aussi appelées études corrélationnelles,

pour comprendre le système (SHADISH et al., 2001). Cela consiste à mesurer une variable d'intérêt (par exemple le nombre d'individus) et des variables dont on souhaite mesurer l'effet sur la variable d'intérêt (par exemple le temps dans le cas de l'estimation d'une tendance de population), puis de calculer leur corrélation. Les études observationnelles sont particulièrement sensibles aux facteurs confondants, et l'inférence causale est souvent très délicate. Par ailleurs, en biologie de la conservation les études observationnelles, et notamment les suivis de population, sont sujettes à deux autres sources d'erreurs : la **variation spatiale** et les **erreurs d'observation** (YOCCOZ et al., 2001).

Pour la plupart des programmes de suivis de population, il est impossible de prendre des mesures sur l'intégralité des unités composant la population statistique, comme par exemple tous les sites de France où une espèce est potentiellement présente. Il est donc nécessaire d'estimer les tendances globales à partir de mesures venant d'échantillons d'unités, par exemple un sous-ensemble de sites de présence potentielle. Pour être certain que les estimations de tendance ne soient pas biaisées, il est nécessaire que l'échantillon soit sélectionné par **échantillonnage probabiliste**, c'est-à-dire que l'échantillon est sélectionné sur la base du hasard au sein d'une population statistique bien définie, chaque unité d'échantillonnage ayant une probabilité de sélection positive connue (COCHRAN, 1977). Au contraire, les estimations ont de fortes chances d'être biaisées si l'échantillon est sélectionné par **échantillonnage de jugement** ("*judgment sampling*" en anglais), c'est-à-dire que l'échantillon est sélectionné avec une certaine intention, par exemple parce qu'on pense qu'il est représentatif de la population sur la base des connaissances actuelles, ou pour des raisons de commodité, par exemple pour limiter la distance à parcourir entre les unités (PETERSON et al., 1999; YOCCOZ et al., 2001). Malgré cela, l'échantillonnage de jugement est couramment utilisé dans les programmes de suivi des populations (ANDERSON, 2001). Par ailleurs, les populations étudiées peuvent présenter une grande diversité de distributions spatiales (par exemple agrégation ou répulsion des individus) et de dynamiques temporelles (par exemple tendances linéaires ou non linéaires). De nombreuses méthodes d'échantillonnage probabiliste ont été développées pour s'adapter à ces caractéristiques, afin d'améliorer la précision des estimations de taille et de tendance de population à taille d'échantillon constante. Une vue d'ensemble des principales méthodes d'échantillonnage (à la fois spatiales et temporelles) est présentée dans le premier chapitre de cette thèse, et

le deuxième chapitre s'intéresse à comment améliorer la précision des estimations de taille de population où les individus sont agrégés dans l'espace, une caractéristique courante des populations de plantes (DAMGAARD & IRVINE, 2019 ; GREIG-SMITH, 1983 ; ROBINSON, 1954).

La deuxième source d'erreur principale des études observationnelles en biologie de la conservation sont les erreurs d'observation. Aucune méthode d'observation ne permet d'avoir des mesures sans aucune erreur, c'est-à-dire parfaitement exactes et sans aucun biais. Les suivis de population se basent généralement sur une forme de comptage, par exemple du nombre de sites occupés par une espèce ou du nombre d'individus dans un échantillon de sites. Pour ce type de mesure, la principale source d'erreur d'observation est la **détection imparfaite**, c'est-à-dire de ne pas toujours détecter une espèce quand elle est présente, ou ne pas détecter tous les individus durant des comptages. Si la détection est imparfaite mais constante dans le temps et l'espace, les estimations faites à un instant t seront sous-estimées, mais les estimations de tendances temporelles ne seront pas biaisées. Par exemple, les tailles de population seront estimées plus petites qu'elles ne le sont en réalité, mais les estimations de tendances de la densité d'individus ne seront pas biaisées (WILLIAMS et al., 2002). Cependant, il suffit d'un changement de 4 à 8% de la probabilité de détection au cours du temps pour que les estimations de tendance soient également biaisées (ARCHAUX et al., 2012). En outre, a priori la détection varie généralement bien plus que de 4-8% dans le temps et l'espace dans le cadre d'études sur les populations de plantes (ALEXANDER et al., 1997 ; CHEN et al., 2013 ; CHEN et al., 2009 ; GARRARD et al., 2013). Pour éviter de tels biais, des outils statistiques ont été développés pour estimer la probabilité de détection (de l'espèce ou des individus selon la variable d'intérêt) et ainsi corriger les estimations des tendances de population (voir par exemple BURNHAM & ANDERSON, 1976 ; MACKENZIE et al., 2002 ; OTIS et al., 1978 ; TYRE et al., 2003). Durant mon doctorat, j'ai conçu et mis en œuvre une expérience à mi-chemin entre une expérience randomisée et une quasi-expérience pour vérifier si la détection des individus est imparfaite lorsque l'on compte des individus de plantes non marquées, ce qui n'avait encore jamais été démontré formellement, et comprendre quelles variables influencent la probabilité de détection des individus. Les résultats de cette expérience sont présentés dans le troisième chapitre de ce manuscrit.

En plus des expériences et des études observationnelles, il existe une troisième approche pour comprendre le fonctionnement d'un système et tester des hypothèses. Il s'agit des **simulations informatiques**, aussi appelées simulations numériques. Cela consiste à créer un programme informatique qui reproduit le fonctionnement d'un système tel qu'on le comprend, c'est-à-dire notre modèle théorique du système (MORGAN, 1984). L'avantage des simulations informatiques est que le système simulé peut être manipulé à volonté, contrairement à la réalité où elles peuvent être limitées pour des raisons éthiques et de coûts. Les simulations peuvent être vues comme un type d'expérience scientifique contrôlée, puisque l'expérimentateur contrôle tout le système étudié, ou comme une expérience de pensée (JEBEILE, 2016 ; PECK, 2004). Le désavantage des simulations est la transposition des résultats obtenus à la réalité. Si le modèle théorique utilisé n'est pas assez réaliste, il est possible que les résultats des simulations ne soient pas valables dans la réalité (GUALA, 2002). Ainsi, un certain nombre de chercheurs et de philosophes des sciences considèrent que les expériences ont une supériorité épistémique sur les simulations (PARKE, 2014 ; ROUSH, 2018). Malgré cela, les simulations sont devenues un outil incontournable dans de nombreux domaines scientifiques, l'opposition initialement perçue entre expériences et simulations s'est réduite avec le temps, et des approches hybrides mêlant expérimentations et simulations sont maintenant courantes (MEYER et al., 2009). Pour l'étude présentée dans le deuxième chapitre de cette thèse, j'ai utilisé des simulations pour comparer la précision des estimations de taille de population obtenues avec trois méthodes d'échantillonnage pour des populations dont les individus étaient plus ou moins spatialement agrégés. J'ai ensuite confirmé les résultats des simulations grâce à des mesures prises sur le terrain sur trois populations de plantes ayant des patrons d'agrégation contrastés.

0.4 Prise de décision et gestion des risques en biologie de la conservation

Comme je l'ai développé dans la partie 1.2 de cette introduction, la biologie de la conservation est née en réponse à la crise de la biodiversité et ses objectifs sont, *in fine*, opérationnels. Les études réalisées visent à déterminer ce qu'il est nécessaire de protéger, quand est-ce qu'il est nécessaire d'intervenir, comment s'y prendre, et à évaluer la

réussite ou non des interventions. Cependant, comme dans toutes les sciences naturelles et particulièrement dans les sciences du vivant, les résultats des études comportent toujours une certaine part d'incertitude. Les décisions (déclencher ou non une intervention, sur quelle population, etc.) doivent être prises malgré cette incertitude, et comportent donc un certain risque d'erreur. Par exemple, un acteur de la conservation peut décider de ne pas protéger une population pourtant en danger d'extinction, car le suivi réalisé a fourni des estimations trop imprécises de la tendance. A l'inverse, des moyens très importants peuvent être investis dans la conservation d'une population, sans se rendre compte que les mesures de conservation sont inefficaces, car les estimations de la tendance de la population sont biaisées. En outre, les événements que l'on cherche à éviter en biologie de la conservation sont souvent graves, par exemple l'extinction d'une population ou d'une espèce peut être irréversible, il est donc nécessaire de chercher à éviter qu'ils ne surviennent.

La **gestion des risques** a fait l'objet de recherches scientifiques, et est généralement désignée sous l'appellation anglaise de « *risk management* ». Au départ, ce domaine de recherche s'intéressait principalement à l'économie (par exemple les cracks boursiers), aux accidents industriels (par exemple les fuites de substances chimiques ou radioactives) et aux catastrophes naturelles (tempêtes, inondations, etc.). Des études se sont ensuite intéressées à d'autres sujets comme l'écotoxicologie et la biologie de la conservation (BURGMAN, 2005). En gestion des risques, un **risque** est défini comme la probabilité d'occurrence d'un événement indésirable durant une fenêtre de temps donnée. La **gravité** d'un événement désigne quant à elle l'importance des conséquences négatives de l'événement sur l'atteinte d'un objectif donné, si jamais il devait survenir. L'illustration la plus simple des concepts de risque et de gravité d'un événement est celle des prévisions météo : le risque qu'il pleuve demain peut être élevé, mais cet événement n'a aucune gravité pour la réalisation d'un travail en intérieur. Pour un objectif donné, le **cycle classique de la gestion des risques** suit les étapes suivantes (BURGMAN, 2005, p.54) :

1. Inventorier les événements indésirables qui pourraient survenir.
2. Estimer la probabilité d'occurrence (risque) de chaque événement et mesurer sa gravité.

3. Décider quelles actions entreprendre pour diminuer les risques ou la gravité des événements.
4. Mesurer l'effet des actions entreprises, et reprendre les étapes 1 à 3 avec les nouvelles informations à disposition.

Si des hypothèses ont dû être faites durant l'évaluation des risques, une étape d'évaluation de la sensibilité des décisions aux hypothèses peut être ajoutée afin de vérifier que les hypothèses n'impactent pas les décisions de manière importante. De nombreuses méthodes ont été développées pour réaliser chaque étape du cycle. Par exemple, la gravité des événements peut être mesurée qualitativement en demandant à des experts de classer les événements indésirables du plus au moins grave, ou quantitativement, par exemple en estimant le coût que représenterait chaque événement pour une collectivité ou une entreprise (COOKE, 1991). De même, de multiples stratégies sont possibles pour décider sur quoi agir, comme par exemple chercher à éviter à tout prix les événements ayant une gravité au-dessus d'un certain seuil, ou utiliser un budget donné pour minimiser l'espérance de la perte liée aux événements indésirables (pour une synthèse des méthodes possibles pour les quatre étapes du cycle de gestion des risques, voir BURGMAN, 2005).

L'**incertitude** de l'évaluation des risques est un enjeu central en gestion des risques, car plus l'incertitude est élevée, plus la **probabilité de commettre des erreurs de décision** est élevée. Deux types d'incertitudes sont distingués en gestion des risques : l'incertitude épistémique et l'incertitude linguistique. L'**incertitude épistémique** est l'incertitude associée à la connaissance du système étudié. Elle peut venir de **cinq sources** : le manque de précision des mesures, le biais des mesures, la variabilité intrinsèque du système étudié, l'incertitude de la méthode d'analyse statistique et la subjectivité de l'analyste lors de l'interprétation des résultats (REGAN et al., 2002). L'**incertitude linguistique** est liée au fait que le langage et le vocabulaire scientifique ne sont pas exacts. Certains termes ou phrases sont vagues, ambigus ou contexte dépendants. Une étude dont les résultats ont une incertitude épistémique faible peut être mal comprise à cause de l'incertitude linguistique, et engendrer des erreurs de décision (BURGMAN, 2005). Malgré son importance (e.g. REGAN et al., 2000), je ne développerai pas davantage les sources d'incertitude linguistique car mes travaux ont uniquement porté sur l'incertitude

épistémique.

En biologie de la conservation, des événements typiques que l'on cherche à éviter sont l'extinction d'une population ou d'une espèce, ou la dégradation d'un écosystème. Ces événements sont généralement évitables, à condition d'intervenir suffisamment tôt et de manière adéquate (GODET & DEVICTOR, 2018 ; MARTIN et al., 2012). Des mesures de mitigation peuvent également parfois être prises pour diminuer la gravité des événements, comme la conservation de graines ex situ qui permet d'être en mesure de réintroduire une espèce si jamais elle venait à s'éteindre dans la nature (LI & PRITCHARD, 2009). Cependant, de telles mesures ne sont pas toujours possibles, et un programme de réintroduction peut s'avérer plus coûteux et hasardeux que d'éviter qu'une population ne s'éteigne (FISCHER & LINDENMAYER, 2000 ; SOORAE, 2016). Améliorer la précision des estimations de taille et de tendance de population, c'est-à-dire réduire l'incertitude associée aux estimations, permet d'améliorer la précision des estimations de probabilité d'extinction (DENNIS et al., 1991 ; ELDERD et al., 2003), ce qui est crucial pour réduire les risques d'erreurs de décision et ainsi améliorer la conservation des populations. En outre, plus les estimations de tendances sont précises, plus il est possible de détecter tôt qu'une population décline, et la mise en oeuvre d'actions de conservation seront alors généralement moins coûteuses et auront plus de chances de réussite si elles sont déclenchées à ce moment-là que si elles sont déclenchées plus tard (MARTIN et al., 2012).

Parmi les cinq sources d'incertitude épistémique, réduire la variabilité du système étudié est impossible dans le cadre d'études observationnelles telles que les suivis de population. L'incertitude de la méthode d'analyse peut être réduite en développant des méthodes statistiques plus robustes et permettant d'améliorer la précision des estimations de taille et tendance de population, et il s'agit d'un sujet de recherche extrêmement actif en écologie (GIMENEZ et al., 2014). Cependant, même les méthodes d'analyse les plus élaborées ne peuvent pas donner d'estimations fiables des paramètres d'intérêt si les données d'entrée sont de trop mauvaise qualité (ZUCKERBERG et al., 2011). Enfin, la subjectivité de l'analyste peut être réduite en demandant à plusieurs personnes d'interpréter indépendamment les résultats d'une analyse. Dans le cadre de suivis de populations, la principale source de biais des mesures est la détection imparfaite. Afin

d'éviter qu'elle n'engendre des estimations biaisées des tailles et des tendances de population, il est nécessaire d'estimer la probabilité de détection, ce qui permet de corriger statistiquement les estimations malgré le biais des mesures. La précision des mesures peut être améliorée en améliorant le processus d'observation, par exemple en standardisant davantage la méthode d'observation, en formant mieux les observateurs ou en augmentant le temps d'observation (ARCHAUX, 2009 ; ARCHAUX et al., 2006). La stratégie d'échantillonnage utilisée peut aussi être un moyen de réduire simultanément plusieurs sources d'incertitude épistémique d'un suivi de population sans augmenter son coût. En effet, concevoir un plan d'échantillonnage adapté aux caractéristiques de la population étudiée peut permettre de compenser l'imprécision des mesures, de réduire l'incertitude de la méthode d'analyse statistique et ainsi la part de subjectivité de l'interprétation des résultats (KISH, 1965).

0.5 Objectifs et questions de recherche

Comme nous avons pu le voir dans cette introduction, les estimations de taille et de tendance de population jouent un rôle central en biologie de la conservation. Réduire l'incertitude de ces estimations permet d'éviter des erreurs de décision et d'optimiser l'utilisation des ressources allouées à la conservation, et ainsi de lutter plus efficacement contre le déclin de la biodiversité. L'objectif général de mes travaux de doctorat était d'améliorer les méthodes de suivi des populations de plantes afin qu'elles puissent fournir des estimations non biaisées et plus précises des tailles et des tendances de population. Pour cela, je me suis intéressé aux deux principaux problèmes méthodologiques des suivis de population : d'une part les plans d'échantillonnage, et d'autre part les erreurs d'observation, et plus spécifiquement la détection imparfaite. Cette thèse s'organise en trois chapitres.

Le dernier guide méthodologique sur les méthodes de suivi des populations de plantes a été publié il y a 25 ans (ELZINGA & SALZER, 1998), et de nombreux développements méthodologiques ont été réalisés depuis, à la fois sur les plans d'échantillonnage et la prise en compte des erreurs d'observation. L'objectif du premier chapitre de ce manuscrit était de faire l'état de l'art des méthodes de suivi des populations végétales, et d'identifier les sujets de recherche prioritaires afin d'améliorer la précision

et réduire le biais des estimations de tendance. En outre, il est apparu au cours de mon étude de la littérature que l'absence de prise en compte des erreurs d'observation dans les suivis de populations de plantes ne semblait pas venir du manque de méthodes disponibles, mais d'un manque de mise en œuvre des méthodes existantes. Ce chapitre a donc également eu pour objectif de vérifier la validité de ce constat, et le cas échéant, de présenter de manière accessible ces méthodes afin d'encourager leur adoption par les botanistes.

Au niveau des plans d'échantillonnage, l'un des problèmes des populations de plantes est que les individus ont une forte tendance à l'agrégation spatiale. Cela engendre une plus forte variabilité entre unités d'échantillonnage que dans des populations où les individus se répartissent de manière homogène dans l'espace, et donc des estimations de taille de population moins précises. L'incertitude des études est donc plus forte pour les populations agrégées que pour les populations spatialement homogènes, pour lesquelles les estimations sont en moyenne plus précises. Le deuxième chapitre s'intéresse à la comparaison de la précision des estimations obtenues avec trois méthodes d'échantillonnage selon le niveau d'agrégation des individus de la population étudiée. En outre, j'y explique le mécanisme à l'origine des différences de précisions entre les méthodes, et propose une manière d'optimiser les plans d'échantillonnage de populations agrégées.

Estimer la taille d'une population de plantes nécessite de compter des individus sur un échantillon d'unités spatiales, et estimer la tendance du nombre d'individus nécessite de répéter ces comptages au cours du temps. Si les comptages sont sujets à la détection imparfaite, cela mène à sous-estimer les tailles de population, et si la détection est hétérogène dans le temps, les estimations de tendance risquent d'être biaisées. La détection imparfaite a déjà été mise en évidence pour la détection d'individus marqués (ALEXANDER et al., 1997; KÉRY & GREGG, 2003), mais n'avait encore jamais été mise en évidence formellement pour les comptages d'individus non marqués, alors que cette métrique est couramment utilisée pour suivre les populations de plantes (REISCH et al., 2018). Le troisième chapitre présente les résultats d'une expérience que j'ai réalisée sur la détection des individus dans le cadre de comptages de plantes non marquées, et s'intéresse aux facteurs observationnels et écologiques influençant la probabilité de

détection.

Références

- ALEXANDER, H. M., SLADE, N. A., & KETTLE, W. D. (1997). Application of mark-recapture models to estimation of the population size of plants. *Ecology*, 78(4), 1230-1237. [https://doi.org/10.1890/0012-9658\(1997\)078\[1230:AOMRMT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1230:AOMRMT]2.0.CO;2) (cf. p. 18, 24)
- ANDERSON, D. R. (2001). The Need to Get the Basics Right in Wildlife Field Studies. *Wildlife Society Bulletin (1973-2006)*, 29(4), 1294-1297 (cf. p. 13, 17).
- ARCHAUX, F. (2009). Could we obtain better estimates of plot species richness from multiple-observer plant censuses? *Journal of Vegetation Science*, 20(4), 603-611. <https://doi.org/10.1111/j.1654-1103.2009.01079.x> (cf. p. 23)
- ARCHAUX, F., GOSSELIN, F., BERGES, L., & CHEVALIER, R. (2006). Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science*, 17(3), 299-306. [https://doi.org/10.1658/1100-9233\(2006\)017\[0299:EOSTSR\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2006)017[0299:EOSTSR]2.0.CO;2) (cf. p. 23)
- ARCHAUX, F., HENRY, P.-Y., & GIMENEZ, O. (2012). When can we ignore the problem of imperfect detection in comparative studies? *Methods in Ecology and Evolution*, 3(1), 188-194. <https://doi.org/10.1111/j.2041-210X.2011.00142.x> (cf. p. 18)
- BALL, P. (2004). *Critical Mass : How One Thing Leads to Another*. Farrar, Straus ; Giroux. (Cf. p. 12).
- BARBAULT, R. (1997). *Biodiversité. Introduction à la biologie de la conservation* (Hachette). (Cf. p. 8, 9).
- BARNOSKY, A. D., MATZKE, N., TOMIYA, S., WOGAN, G. O. U., SWARTZ, B., QUENTAL, T. B., MARSHALL, C., MCGUIRE, J. L., LINDSEY, E. L., MAGUIRE, K. C., MERSEY, B., & FERRER, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471(7336), 51-57. <https://doi.org/10.1038/nature09678> (cf. p. 4, 5)
- BAYON, G., DENNIELOU, B., ETOUBLEAU, J., PONZEVEVA, E., TOUCANNE, S., & BERMELL, S. (2012). Intensifying Weathering and Land Use in Iron Age Central Africa. *Science*, 335(6073), 1219-1222. <https://doi.org/10.1126/science.1215400> (cf. p. 5)
- BRIÈRE, J.-F. (1990). *La pêche française en Amérique du Nord au XVIIIe siècle*. Fides. (Cf. p. 2).
- BURGMAN, M. (2005). *Risks and Decisions for Conservation and Environmental Management*. Cambridge University Press. (Cf. p. 9, 20, 21).
- BURNHAM, K. P., & ANDERSON, D. R. (1976). Mathematical Models for Nonparametric Inferences from Line Transect Data. *Biometrics*, 32(2), 325-336. <https://doi.org/10.2307/2529501> (cf. p. 18)
- CAMPBELL, D. T., & STANLEY, J. (1963). *Experimental and Quasi-Experimental Designs for Research* (1st edition). Cengage Learning. (Cf. p. 16).
- CARSON, R. (1962). *Silent Spring*. Houghton Mifflin Company. (Cf. p. 2).
- CAZALIS, V., LOREAU, M., & BARRAGAN-JASON, G. (2023). A global synthesis of trends in human experience of nature. *Frontiers in Ecology and the Environment*, n/a(n/a). <https://doi.org/10.1002/fee.2540> (cf. p. 4)

- CHEN, G., KÉRY, M., PLATTNER, M., MA, K., & GARDNER, B. (2013). Imperfect detection is the rule rather than the exception in plant distribution studies. *Journal of Ecology*, 101(1), 183-191. <https://doi.org/10.1111/1365-2745.12021> (cf. p. 18)
- CHEN, G., KÉRY, M., ZHANG, J., & MA, K. (2009). Factors affecting detection probability in plant distribution studies. *Journal of Ecology*, 97(6), 1383-1389. <https://doi.org/10.1111/j.1365-2745.2009.01560.x> (cf. p. 18)
- COCHRAN, W. G. (1977). *Sampling Techniques* (3rd). John Wiley & Sons. (Cf. p. 12, 17).
- COLLEN, B., LOH, J., WHITMEE, S., MCRAE, L., AMIN, R., & BAILLIE, J. E. M. (2009). Monitoring Change in Vertebrate Abundance : the Living Planet Index. *Conservation Biology*, 23(2), 317-327. <https://doi.org/10.1111/j.1523-1739.2008.01117.x> (cf. p. 5)
- COOKE, R. M. (1991). *Experts in Uncertainty : Opinion and Subjective Probability in Science*. Oxford University Press. (Cf. p. 21).
- COPI, I., COHEN, C., & FLAGE, D. (2006). *Essentials of Logic* (2nd edition). Routledge. (Cf. p. 14).
- COURCHAMP, F., CLUTTON-BROCK, T., & GRENFELL, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution*, 14(10), 405-410. [https://doi.org/10.1016/S0169-5347\(99\)01683-3](https://doi.org/10.1016/S0169-5347(99)01683-3) (cf. p. 8)
- CRAWLEY, M. J., ROSS, G. J. S., HASSELL, M. P., & MAY, R. M. (1990). The population dynamics of plants. *Philosophical Transactions of the Royal Society of London. Series B : Biological Sciences*, 330(1257), 125-140. <https://doi.org/10.1098/rstb.1990.0187> (cf. p. 11)
- DAGNELIE, P. (1982). Diversité et unité de la statistique. *Journal de la Société de statistique de Paris*, 123(2), 86-92 (cf. p. 12).
- DAMGAARD, C. F., & IRVINE, K. M. (2019). Using the beta distribution to analyse plant cover data. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13200> (cf. p. 18)
- DENNIS, B., MUNHOLLAND, P. L., & SCOTT, J. M. (1991). Estimation of Growth and Extinction Parameters for Endangered Species. *Ecological Monographs*, 61(2), 115-143. <https://doi.org/10.2307/1943004> (cf. p. 22)
- DINARDO, J. (2008). Natural Experiments and Quasi-Natural Experiments. In *Microeconometrics* (p. 139-153). Palgrave Macmillan UK. https://doi.org/10.1057/9780230280816_18. (Cf. p. 15)
- DUNN, R. (2012). In retrospect : Silent Spring. *Nature*, 485(7400), 578-579. <https://doi.org/10.1038/485578a> (cf. p. 2)
- EINSTEIN, A., & INFELD, L. (1966). *The evolution of physics : from early concepts to relativity and quanta*. New York : Simon ; Schuster. (Cf. p. 15).
- ELDERD, B. D., SHAHANI, P., & DOAK, D. F. (2003). The Problems and Potential of Count-Based Population Viability Analyses. In C. A. BRIGHAM & M. W. SCHWARTZ (Éd.), *Population Viability in Plants : Conservation, Management, and Modeling of Rare Plants* (p. 173-202). Springer. https://doi.org/10.1007/978-3-662-09389-4_7. (Cf. p. 22)
- ELZINGA, C. L., & SALZER, D. W. (1998). *Measuring & Monitoring Plant Populations*. U.S. Department of the Interior, Bureau of Land Management. (Cf. p. 23).
- FAO. (2019). *The State of the World's Biodiversity for Food and Agriculture*. (Cf. p. 7).
- FERRARO, P. J., & HANAUER, M. M. (2014). Advances in Measuring the Environmental and Social Impacts of Environmental Programs. *Annual Review of Environment and Resources*, 39(1), 495-517. <https://doi.org/10.1146/annurev-environ-101813-013230> (cf. p. 16)

- FISCHER, J., & LINDENMAYER, D. B. (2000). An assessment of the published results of animal relocations. *Biological Conservation*, 96(1), 1-11. [https://doi.org/10.1016/S0006-3207\(00\)00048-3](https://doi.org/10.1016/S0006-3207(00)00048-3) (cf. p. 22)
- FISCHER, M., & MATTHIES, D. (1998). RAPD variation in relation to population size and plant fitness in the rare *Gentianella germanica* (Gentianaceae). *American Journal of Botany*, 85(6), 811-819. <https://doi.org/10.2307/2446416> (cf. p. 8)
- FISHER, S. R. A. (1935). *The Design of Experiments*. Oliver ; Boyd. (Cf. p. 16).
- FRANKLIN, B. (1755). *Observations Concerning the Increase of Mankind, Peopling of Countries, etc.* Tarrytown, N.Y., Reprinted, W. Abbatt. (Cf. p. 10).
- GARRARD, G. E., MCCARTHY, M. A., WILLIAMS, N. S. G., BEKESSY, S. A., & WINTLE, B. A. (2013). A general model of detectability using species traits. *Methods in Ecology and Evolution*, 4(1), 45-52. <https://doi.org/10.1111/j.2041-210x.2012.00257.x> (cf. p. 18)
- GASTON, K. J., JACKSON, S. F., NAGY, A., CANTÚ-SALAZAR, L., & JOHNSON, M. (2008). Protected Areas in Europe. *Annals of the New York Academy of Sciences*, 1134(1), 97-119. <https://doi.org/10.1196/annals.1439.006> (cf. p. 10)
- GAUCH, H. G. (2002). *Scientific Method in Practice*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511815034>. (Cf. p. 15)
- GIMENEZ, O., BUCKLAND, S. T., MORGAN, B. J. T., BEZ, N., BERTRAND, S., CHOQUET, R., DRAY, S., ETIENNE, M.-P., FEWSTER, R., GOSSELIN, F., MÉRIGOT, B., MONESTIEZ, P., MORALES, J. M., MORTIER, F., MUNOZ, F., OVASKAINEN, O., PAVOINE, S., PRADEL, R., SCHURR, F. M., ... REXSTAD, E. (2014). Statistical ecology comes of age. *Biology Letters*, 10(12), 20140698. <https://doi.org/10.1098/rsbl.2014.0698> (cf. p. 12, 22)
- GODET, L., & DEVICTOR, V. (2018). What Conservation Does. *Trends in Ecology & Evolution*, 33(10), 720-730. <https://doi.org/10.1016/j.tree.2018.07.004> (cf. p. 22)
- GODET, L., DEVICTOR, V., & JIGUET, F. (2007). Estimating relative population size included within protected areas. *Biodiversity and Conservation*, 16(9), 2587-2598. <https://doi.org/10.1007/s10531-006-9020-2> (cf. p. 10)
- GRAND, J., CUMMINGS, M. P., REBELO, T. G., RICKETTS, T. H., & NEEL, M. C. (2007). Biased data reduce efficiency and effectiveness of conservation reserve networks. *Ecology Letters*, 10(5), 364-374. <https://doi.org/10.1111/j.1461-0248.2007.01025.x> (cf. p. 14)
- GRAUNT, J. (1662). *Natural and Political Observations Made upon the Bills of Mortality*. (Cf. p. 12).
- GREEN, R. H. (1979). *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley & Sons. (Cf. p. 16).
- GREIG-SMITH, P. (1983). *Quantitative Plant Ecology*. University of California Press. (Cf. p. 18).
- GRIER, J. W. (1982). Ban of DDT and Subsequent Recovery of Reproduction in Bald Eagles. *Science*, 218(4578), 1232-1235. <https://doi.org/10.1126/science.7146905> (cf. p. 3, 10)
- GUALA, F. (2002). Models, Simulations, and Experiments. In L. MAGNANI & N. J. NERSESSIAN (Éd.), *Model-Based Reasoning : Science, Technology, Values* (p. 59-74). Springer US. https://doi.org/10.1007/978-1-4615-0605-8_4. (Cf. p. 19)
- HALLMANN, C. A., SORG, M., JONGEJANS, E., SIEPEL, H., HOFLAND, N., SCHWAN, H., STENMANS, W., MÜLLER, A., SUMSER, H., HÖRREN, T., GOULSON, D., & KROON, H. d. (2017). More than 75 percent decline over 27 years in total flying

- insect biomass in protected areas. *PLOS ONE*, 12(10), e0185809. <https://doi.org/10.1371/journal.pone.0185809> (cf. p. 3)
- HAMILTON, L. C., HAEDRICH, R. L., & DUNCAN, C. M. (2004). Above and Below the Water : Social/Ecological Transformation in Northwest Newfoundland. *Population and Environment*, 25(3), 195-215. <https://doi.org/10.1007/s11111-004-4484-z> (cf. p. 2)
- HARDIN, G. (1968). The Tragedy of the Commons. *Science*, 162(3859), 1243-1248. <https://doi.org/10.1126/science.162.3859.1243> (cf. p. 4)
- HARPER, J. L. (1967). A Darwinian Approach to Plant Ecology. *Journal of Ecology*, 55(2), 247-270. <https://doi.org/10.2307/2257876> (cf. p. 11)
- HARPER, J. L., & WHITE, J. (1974). The Demography of Plants. *Annual Review of Ecology and Systematics*, 5, 419-463 (cf. p. 10, 11).
- HARPER, J. L., WILLIAMS, J. T., & SAGAR, G. R. (1965). The Behaviour of Seeds in Soil : I. The Heterogeneity of Soil surfaces and its Role in Determining the Establishment of Plants from Seed. *Journal of Ecology*, 53(2), 273-286. <https://doi.org/10.2307/2257975> (cf. p. 11)
- HARPER, J. (1964). The individual in the population. *Journal of Ecology*, 52, 149-158 (cf. p. 11).
- HARPER, J. L. (1977). *Population Biology of Plants*. Academic Press. (Cf. p. 11).
- HOGUE, A. S., & BREON, K. (2022). The greatest threats to species. *Conservation Science and Practice*, 4(5), e12670. <https://doi.org/10.1111/csp2.12670> (cf. p. 6)
- HORNADAY, W. T. (1889). *The Extermination of the American Bison*. U.S. Government Printing Office. (Cf. p. 7).
- HUNTER, M. L., & GIBBS, J. P. (2006). *Fundamentals of Conservation Biology*. John Wiley & Sons. (Cf. p. 8).
- IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (rapp. tech.). Zenodo. <https://doi.org/10.5281/zenodo.6417333>. (Cf. p. 4, 6)
- IUCN. (2019). Guidelines for Using the IUCN Red List Categories and Criteria - Version 14. (Cf. p. 9).
- IUCN. (2022). The IUCN Red List of Threatened Species. (Cf. p. 5).
- JEBEILE, J. (2016). Are simulations the digital experiences? *Dialogue-Canadian Philosophical Review*, 55(1), 59-86. <https://doi.org/10.1017/S0012217315001122> (cf. p. 19)
- KÉRY, M., & GREGG, K. B. (2003). Effects of life-state on detectability in a demographic study of the terrestrial orchid *Cleistes bifaria*. *Journal of Ecology*, 91(2), 265-273. <https://doi.org/10.1046/j.1365-2745.2003.00759.x> (cf. p. 24)
- KISH, L. (1965). *Survey Sampling*. John Wiley & Sons. (Cf. p. 23).
- KOCH, P. L., & BARNOSKY, A. D. (2006). Late Quaternary Extinctions : State of the Debate. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 215-250. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132415> (cf. p. 5)
- KUHN, T. S. (1962). *The Structure of Scientific Revolutions*. University of Chicago Press. (Cf. p. 15).
- LAVERGNE, S., THUILLER, W., MOLINA, J., & DEBUSSCHE, M. (2005). Environmental and human factors influencing rare plant local occurrence, extinction and persistence : a 115-year study in the Mediterranean region. *Journal of Biogeography*, 32(5), 799-811. <https://doi.org/10.1111/j.1365-2699.2005.01207.x> (cf. p. 6)

- LEGG, C. J., & NAGY, L. (2006). Why most conservation monitoring is, but need not be, a waste of time. *Journal of Environmental Management*, 78(2), 194-199. <https://doi.org/10.1016/j.jenvman.2005.04.016> (cf. p. 13)
- LI, D.-Z., & PRITCHARD, H. W. (2009). The science and economics of ex situ plant conservation. *Trends in Plant Science*, 14(11), 614-621. <https://doi.org/10.1016/j.tplants.2009.09.005> (cf. p. 22)
- LINCOLN, F. C. (1930). *Calculating waterfowl abundance on the basis of banding returns*. Washington, D.C. : U.S. Dept. of Agriculture. (Cf. p. 10).
- LINDENMAYER, D. B., & LIKENS, G. E. (2009). Adaptive monitoring : a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution*, 24(9), 482-486. <https://doi.org/10.1016/j.tree.2009.03.005> (cf. p. 13)
- LISTER, B. C., & GARCIA, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences*, 115(44), E10397-E10406. <https://doi.org/10.1073/pnas.1722477115> (cf. p. 3)
- MACKENZIE, D. I., NICHOLS, J. D., LACHMAN, G. B., DROEGE, S., ROYLE, J. A., & LANGTIMM, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248-2255. <https://doi.org/10.2307/3072056> (cf. p. 18)
- MALTHUS, T. R. (R. (1798). *An essay on the principle of population, as it affects the future improvement of society. With remarks on the speculations of Mr. Godwin, M. Condorcet and other writers*. London, J. Johnson. (Cf. p. 10).
- MARTIN, T. G., NALLY, S., BURBIDGE, A. A., ARNALL, S., GARNETT, S. T., HAYWARD, M. W., LUMSDEN, L. F., MENKHORST, P., MCDONALD-MADDEN, E., & POSSINGHAM, H. P. (2012). Acting fast helps avoid extinction. *Conservation Letters*, 5(4), 274-280. <https://doi.org/10.1111/j.1755-263X.2012.00239.x> (cf. p. 22)
- MCDONALD-MADDEN, E., BAXTER, P. W. J., FULLER, R. A., MARTIN, T. G., GAME, E. T., MONTAMBAULT, J., & POSSINGHAM, H. P. (2010). Monitoring does not always count. *Trends in Ecology & Evolution*, 25(10), 547-550. <https://doi.org/10.1016/j.tree.2010.07.002> (cf. p. 13)
- MEYER, K. M., MOOIJ, W. M., VOS, M., HOL, W. H. G., & van der PUTTEN, W. H. (2009). The power of simulating experiments. *Ecological Modelling*, 220(19), 2594-2597. <https://doi.org/10.1016/j.ecolmodel.2009.06.001> (cf. p. 19)
- MØLLER, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, 9(11), 6581-6587. <https://doi.org/10.1002/ece3.5236> (cf. p. 3)
- MORGAN, B. J. T. (1984). *Elements of Simulation*. Routledge. (Cf. p. 19).
- MPO. (2021). *Évaluation du stock de morue dans la sous-division 3Ps de l'OPANO* (rapp. tech. N° 2021/031). Secrétariat canadien de consultation scientifique. (Cf. p. 2).
- MTE. (2022). *Stratégie Nationale Biodiversité 2030 - 1er volet pré-COP15* (rapp. tech.). Ministère de la Transition Ecologique. (Cf. p. 8).
- NATIONS UNIES. (1992). *Convention sur la Diversité Biologique*. (Cf. p. 7).
- NICHOLS, J. D., & WILLIAMS, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution*, 21(12), 668-673. <https://doi.org/10.1016/j.tree.2006.08.007> (cf. p. 13)
- OGDEN, J. (1985). An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany*, 23(4), 751-772. <https://doi.org/10.1080/0028825X.1985.10434241> (cf. p. 11)

- OLLERTON, J., WINFREE, R., & TARRANT, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120(3), 321-326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x> (cf. p. 6)
- OTIS, D. L., BURNHAM, K. P., WHITE, G. C., & ANDERSON, D. R. (1978). Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs*, (62), 3-135 (cf. p. 18).
- PARKE, E. C. (2014). Experiments, Simulations, and Epistemic Privilege. *Philosophy of Science*, 81(4), 516-536. <https://doi.org/10.1086/677956> (cf. p. 19)
- PARKER, R. A. (1950). *The Calendars of Ancient Egypt*. University of Chicago Press. (Cf. p. 12).
- PAULY, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, 10(10), 430. [https://doi.org/10.1016/S0169-5347\(00\)89171-5](https://doi.org/10.1016/S0169-5347(00)89171-5) (cf. p. 4)
- PECK, S. L. (2004). Simulation as experiment : a philosophical reassessment for biological modeling. *Trends in Ecology & Evolution*, 19(10), 530-534. <https://doi.org/10.1016/j.tree.2004.07.019> (cf. p. 19)
- PETERSON, S. A., URQUHART, N. S., & WELCH, E. B. (1999). Sample Representativeness : A Must for Reliable Regional Lake Condition Estimates. *Environmental Science & Technology*, 33(10), 1559-1565. <https://doi.org/10.1021/es9807111> (cf. p. 17)
- PIMM, S. L., JENKINS, C. N., ABELL, R., BROOKS, T. M., GITTLEMAN, J. L., JOPPA, L. N., RAVEN, P. H., ROBERTS, C. M., & SEXTON, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344(6187), 1246752. <https://doi.org/10.1126/science.1246752> (cf. p. 4, 5)
- PLATT, J. R. (1964). Strong Inference. *Science*, 146(3642), 347-353. <https://doi.org/10.1126/science.146.3642.347> (cf. p. 15)
- POPESCU, V. D., ROZYLOWICZ, L., NICULAE, I. M., CUCU, A. L., & HARTEL, T. (2014). Species, Habitats, Society : An Evaluation of Research Supporting EU's Natura 2000 Network. *PLOS ONE*, 9(11), e113648. <https://doi.org/10.1371/journal.pone.0113648> (cf. p. 8)
- PRIMACK, R. B., SARRAZIN, F., & LECOMTE, J. (2012). *Biologie de la conservation*. Dunod. (Cf. p. 9).
- PYNEGAR, E. L., GIBBONS, J. M., ASQUITH, N. M., & JONES, J. P. G. (2021). What role should randomized control trials play in providing the evidence base for conservation? *Oryx*, 55(2), 235-244. <https://doi.org/10.1017/S0030605319000188> (cf. p. 16)
- REGAN, H. M., COLYVAN, M., & BURGMAN, M. A. (2000). A proposal for fuzzy International Union for the Conservation of Nature (IUCN) categories and criteria. *Biological Conservation*, 92(1), 101-108. [https://doi.org/10.1016/S0006-3207\(99\)00060-9](https://doi.org/10.1016/S0006-3207(99)00060-9) (cf. p. 21)
- REGAN, H. M., COLYVAN, M., & BURGMAN, M. A. (2002). A Taxonomy and Treatment of Uncertainty for Ecology and Conservation Biology. *Ecological Applications*, 12(2), 618-628. [https://doi.org/10.1890/1051-0761\(2002\)012\[0618:ATATOU\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0618:ATATOU]2.0.CO;2) (cf. p. 21)
- REICHARDT, C. S. (2019). *Quasi-Experimentation : A Guide to Design and Analysis* (1st edition). The Guilford Press. (Cf. p. 16).
- REID, W. V. (2005). *Ecosystems and Human Well-Being - A Report of the Millennium Ecosystem Assessment* (rapp. tech.). Washington DC : Millennium Ecosystem Assessment Board. (Cf. p. 7).

- REISCH, C., SCHMID, C., & HARTIG, F. (2018). A comparison of methods for estimating plant population size. *Biodiversity and Conservation*, 27(8), 2021-2028. <https://doi.org/10.1007/s10531-018-1522-1> (cf. p. 24)
- REY, O. (2016). *Quand le monde s'est fait nombre*. Stock. (Cf. p. 12).
- RHODES, C. J. (2018). Pollinator Decline – An Ecological Calamity in the Making? *Science Progress*, 101(2), 121-160. <https://doi.org/10.3184/003685018X15202512854527> (cf. p. 3, 6)
- RIPPLE, W. J., & BESCHTA, R. L. (2012). Trophic cascades in Yellowstone : The first 15 years after wolf reintroduction. *Biological Conservation*, 145(1), 205-213. <https://doi.org/10.1016/j.biocon.2011.11.005> (cf. p. 6)
- ROBINSON, P. (1954). The Distribution of Plant Populations. *Annals of Botany*, 18(69), 35-45. <https://doi.org/10.1093/oxfordjournals.aob.a083380> (cf. p. 18)
- ROUSH, S. (2018). The epistemic superiority of experiment to simulation. *Synthese*, 195(11), 4883-4906. <https://doi.org/10.1007/s11229-017-1431-y> (cf. p. 19)
- SANDOM, C., FAURBY, S., SANDEL, B., & SVENNING, J.-C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B : Biological Sciences*, 281(1787), 20133254. <https://doi.org/10.1098/rspb.2013.3254> (cf. p. 5)
- SARUKHAN, J., & HARPER, J. L. (1973). Studies on Plant Demography : *Ranunculus Repens* L., *R. Bulbosus* L. and *R. Acris* L. : I. Population Flux and Survivorship. *Journal of Ecology*, 61(3), 675-716. <https://doi.org/10.2307/2258643> (cf. p. 11)
- SCHELL, C. O., REILLY, M., ROSLING, H., PETERSON, S., & MIA EKSTRÖM, A. (2007). Socioeconomic determinants of infant mortality : A worldwide study of 152 low-, middle-, and high-income countries. *Scandinavian Journal of Public Health*, 35(3), 288-297. <https://doi.org/10.1080/14034940600979171> (cf. p. 10)
- SELLS, S., BASSING, S., BARKER, K., FORSHEE, S., KEEVER, A., GOERZ, J., & MITCHELL, M. (2018). Increased scientific rigor will improve reliability of research and effectiveness of management. *The Journal of Wildlife Management*, 82. <https://doi.org/10.1002/jwmg.21413> (cf. p. 14)
- SHADISH, W. R., COOK, T. D., & CAMPBELL, D. T. (2001). *Experimental and Quasi-Experimental Designs for Generalized Causal Inference* (2nd edition). Cengage Learning. (Cf. p. 15-17).
- SHER, A., & PRIMACK, R. (2019). *An Introduction to Conservation Biology* (Second Edition, Second Edition). Oxford University Press. (Cf. p. 7).
- SIMBERLOFF, D. (1988). The Contribution of Population and Community Biology to Conservation Science. *Annual Review of Ecology and Systematics*, 19, 473-511. <https://doi.org/10.1146/annurev.ecolsys.19.1.473> (cf. p. 12)
- SMOKOROWSKI, K. E., & RANDALL, R. G. (2017). Cautions on using the Before-After-Control-Impact design in environmental effects monitoring programs. *FA-CETS*. <https://doi.org/10.1139/facets-2016-0058> (cf. p. 16)
- SOGA, M., & GASTON, K. J. (2018). Shifting baseline syndrome : causes, consequences, and implications. *Frontiers in Ecology and the Environment*, 16(4), 222-230. <https://doi.org/10.1002/fee.1794> (cf. p. 4)
- SOORAE, P. (2016). *Global Re-introduction Perspectives : 2016 Case-studies from around the globe*. (Cf. p. 22).
- SOULÉ, M. E. (1985). What is Conservation Biology? *BioScience*, 35(11), 727-734. <https://doi.org/10.2307/1310054> (cf. p. 8, 12)

- TYRE, A. J., TENHUMBERG, B., FIELD, S. A., NIEJALKE, D., PARRIS, K., & POSSINGHAM, H. P. (2003). Improving Precision and Reducing Bias in Biological Surveys : Estimating False-Negative Error Rates. *Ecological Applications*, 13(6), 1790-1801. <https://doi.org/https://doi.org/10.1890/02-5078> (cf. p. 18)
- UPTON, G., & COOK, I. (2008). *A Dictionary of Statistics*. Oxford University Press. (Cf. p. 11).
- WAGNER, D. L. (2020). Insect Declines in the Anthropocene. *Annual Review of Entomology*, 65(1), 457-480. <https://doi.org/10.1146/annurev-ento-011019-025151> (cf. p. 3)
- WALTERS, C., & MAGUIRE, J.-J. (1996). Lessons for stock assessment from the northern cod collapse. *Reviews in Fish Biology and Fisheries*, 6(2), 125-137. <https://doi.org/10.1007/BF00182340> (cf. p. 2)
- WATSON, J., & ESTES, J. A. (2011). Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs*, 81(2), 215-239. <https://doi.org/10.1890/10-0262.1> (cf. p. 6)
- WILLIAMS, B. K., NICHOLS, J. D., & CONROY, M. J. (2002). *Analysis and Management of Animal Populations : Modeling, Estimation, and Decision Making*. Academic Press. (Cf. p. 13, 18).
- WWF. (2020). *Living Planet Report 2022 – Building a nature-positive society* (rapp. tech.). WWF. Gland, Switzerland. (Cf. p. 5, 9).
- YOCOZ, N. G., NICHOLS, J. D., & BOULINIER, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16(8), 446-453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4) (cf. p. 13, 17)
- ZUCKERBERG, B., HUETTMANN, F., & FRAIR, J. (2011). Proper Data Management as a Scientific Foundation for Reliable Species Distribution Modeling. In C. A. DREW, Y. F. WIERSMA & F. HUETTMANN (Éd.), *Predictive Species and Habitat Modeling in Landscape Ecology : Concepts and Applications* (p. 45-70). Springer. https://doi.org/10.1007/978-1-4419-7390-0_4. (Cf. p. 22)



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Chapitre 1

Suivi des populations végétales : frontières des connaissances actuelles et défis méthodologiques à venir

Le premier chapitre de cette thèse présente l'état actuel des connaissances sur les méthodes de suivi des populations végétales, identifie les sujets de recherche méthodologique prioritaires pour améliorer les suivis, et souligne les différences entre les manques de mise en œuvre de méthodes existantes et les lacunes de développement méthodologique. En outre, ce premier chapitre pose les bases conceptuelles des chapitres suivants de la thèse, notamment en ce qui concerne la théorie de l'échantillonnage et la prise en compte des erreurs d'observation, qui seront traitées respectivement dans les chapitres 2 et 3. L'article de review correspondant à ce premier chapitre n'a pas encore été publié et sera soumis après le rendu de mon manuscrit de thèse.

Monitoring plant populations : frontiers of current knowledge and methodological challenges ahead

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Abstract

1. Ecologists monitor populations to study the impact of biotic interactions and abiotic factors on population dynamics, and how changes in populations affect ecosystems. Conservationists need population monitoring to estimate extinction risks, trigger conservation actions and subsequently measure their effectiveness. However, despite its central role in both ecological research and conservation biology, monitoring programmes suffer from recurrent methodological issues that jeopardise their chances of success, especially when monitoring plant populations.
2. We review the methodological literature to provide an up-to-date synthesis of the state of knowledge on methods for monitoring plant populations. We focus on the two main challenges of monitoring populations : building the sampling design and accounting for observation errors, both when the monitoring is carried out at the population and the individual level.
3. Several sampling methods exist to address the main challenges of studying plant populations at a given point in time, i.e. spatial aggregation and rarity, but their extension into the temporal dimension to estimate trends is sometimes lacking. Over the last decades, there has been increasing evidence that despite plants' sessile nature, the main source of observation errors is imperfect detection, whatever the metric used and the measurement method. Many of the methods developed to deal with imperfect detection in vertebrate studies are perfectly applicable to plant populations, and new methods have recently been developed specifically for plants, yet they are seldom used. There seems to be a lack of awareness of the adverse consequences of imperfect detection on study results among plant ecologists.
4. We argue that it is high time that plant ecologists adopt methods to explicitly account for imperfect detection in plant population monitoring studies. We also highlight promising methodological avenues requiring further research, such as the use of drone imagery and machine learning to track individuals over time, and estimating the contribution of seed banks to population dynamics from population-level monitoring data. Moreover, data integration and integrated population models have yet never been used for plants, despite the maturity of these methods

and two decades of extremely fruitful developments.

Keywords— capture-recapture - demography - detectability - extinction risk - long-term survey - population dynamics - sampling design - statistical power

1.1 Introduction

In ecology and conservation biology, the term ‘monitoring’ designates the process of gathering information about a **STATE VARIABLE*** of a system on multiple occasions in order to measure how the system changes over time (YOCCOZ et al., 2001). The monitored systems can be at any organisation level of the living world, from the biosphere to ecosystems, communities and populations. A large diversity of state variables can be targeted, such as the amount of carbon fixed by an ecosystem, a community’s species richness, or a population’s size. Monitoring is fundamental in ecological research to understand the processes occurring over long time scales and how systems respond to environmental drivers (LINDENMAYER et al., 2012). In conservation biology, the main goals of monitoring are to alert if a system leaves a desired state and to measure the effect of perturbations, management actions, or environmental policies (LEGG & NAGY, 2006; LOVETT et al., 2007).

At the population level, ecologists use monitoring to identify the biotic interactions and abiotic factors that shape population dynamics (BJØRNSTAD & GRENFELL, 2001) and understand the consequences of population dynamics on ecosystems, as in biological invasions (SIMBERLOFF et al., 2013) or with the reintroduction of keystone species (RIPPLE & BESCHTA, 2012; WATSON & ESTES, 2011). Population monitoring is also crucial in conservation biology, as it is necessary to assess the extinction risk of species (DENNIS et al., 1991) and inform international conservation policies such as Red Lists (IUCN, 2019). At a more local scale, monitoring a population allows to trigger salvage interventions if a decline is detected and subsequently to measure the effectiveness of the undertaken actions (WILLIAMS et al., 2002).

Despite the importance of monitoring, controversies have arisen in the scientific literature about the effectiveness of monitoring programmes, especially those intended for ‘surveillance’ in conservation (NICHOLS & WILLIAMS, 2006). Some authors state

that many monitoring programmes are inefficient, seldom achieve their goals and waste conservation resources (ANDERSON, 2001; LINDENMAYER & LIKENS, 2009). Many programmes lack precise objectives and are consequently poorly designed (LINDENMAYER et al., 2012), for instance, by being under-dimensioned for the **STATISTICAL POWER*** required to provide meaningful results (LEGG & NAGY, 2006). Another cause of lack of power is measuring many variables to eventually answer multiple questions, at the expense of data quality (LINDENMAYER & LIKENS, 2009). In addition to these issues, two recurrent methodological problems jeopardise the success of many monitoring programmes : using **JUDGEMENT SAMPLING*** instead of **PROBABILITY SAMPLING*** and not accounting for **OBSERVATION ERRORS*** (YOCCOZ et al., 2001). As it is almost always impossible to collect measurements on the entire **STATISTICAL POPULATION***, most monitoring programmes are based on sampling, i.e. information on the state variable is collected on a subset of units from which the change of the state variable of interest is estimated. Although judgement sampling usually results in substantially biased estimates (PETERSON et al., 1999), it is still commonly used (SMITH et al., 2017). Using probability sampling ensures unbiased estimates, but choosing the appropriate sampling design is difficult, as different designs provide variable statistical power depending on the characteristics of the statistical population studied (COCHRAN, 1977). Moreover, observation errors can lead to spurious results if not accounted for, even though a monitoring programme uses probability sampling (ARCHAUX et al., 2012).

Population monitoring can be carried out either at the level of individuals, by monitoring through time the fate of a sample of individuals, or directly at the population level, by measuring a given population **METRIC*** on spatial units, such as the occurrence or density of individuals. In individual monitoring, the state variables of interest are usually **DEMOGRAPHIC PARAMETERS***, such as survival probability or recruitment rate (LEBRETON et al., 1992), but population size can also be estimated (OTIS et al., 1978). When monitoring is conducted at the population level, the aim is to estimate the variation over time of state variables, such as the density of individuals or the species distribution. For both the individual and population levels, the most common type of observation error is **IMPERFECT DETECTION***, i.e. missing individuals during the survey. If detection is imperfect but constant over time and space, the value of

the state variable will be underestimated, e.g., the population will be estimated smaller than it is, but differences measured over time or space will be unbiased (WILLIAMS et al., 2002). However, differences in detection (between sampling occasions or units) as small as 4-8% are sufficient to generate biased estimates (ARCHAUX et al., 2012). Many studies have shown that detection probability usually varies much more than this across time and space (e.g. CHEN et al., 2013; COUTURIER et al., 2013; KÉRY et al., 2009). Statistical tools modelling the observation process have been developed to avoid detection-induced biases. They allow the estimation of the detection probability and provide unbiased estimates. Such development has risen from animal studies, where the capacity of individuals to hide from observers intuitively induces the idea of imperfect detection (see the pioneering work of LINCOLN (1930) and PETERSEN (1896) at the population level, and of CORMACK (1964), JOLLY (1965) and SEBER (1965) at the individual level). However, recent studies have highlighted similar issues when surveying sessile organisms (BERBERICH et al., 2016; DELANEY & LEUNG, 2010), particularly for plants (ALEXANDER et al., 1997; CHEN et al., 2013; CHEN et al., 2009; PERRET et al., 2023).

With about 40% of currently known species considered threatened with extinction (NIC LUGHADHA et al., 2020), tracheophytes (hereafter 'plants') are among the most threatened taxa in the world, making it essential to study population dynamics and their driving factors. Although their sessile nature should facilitate the monitoring of populations, many plant species are difficult to monitor due to complex life cycles (e.g. pioneer or eclipsing species, see GAZAIX et al., 2020) or great spatial rarity (LAVERGNE et al., 2004). These specificities raise methodological challenges for both individual and population-level monitoring programmes. Furthermore, while estimating detection probability has become a standard practice of population monitoring programmes for many animal taxa, it is still seldom done in plant studies (KELLNER & SWIHART, 2014). However, several studies have shown that imperfect detection is the rule for plants. In addition, the last methodological guide on plant population monitoring was published 25 years ago (ELZINGA & SALZER, 1998), and numerous major methodological developments have been made since then regarding both sampling designs (e.g. GUISAN et al., 2006; STEVENS & OLSEN, 2004) and the estimation of detection probability (e.g. GARRARD et al., 2008; MACKENZIE et al., 2002; ROYLE, 2004; TYRE et al., 2003).

This review proposes an up-to-date synthesis that emphasises implementing recent methodological developments to plant surveys to tackle sampling and observation issues. Our first objective was to provide an accessible overview of the current state of knowledge on the methods used for monitoring plant populations. In this section, we have structured our synthesis around the two main methodological challenges faced by monitoring programmes, i.e. the sampling design and the observation errors, and the two levels at which monitoring can be carried out, i.e. population and individual monitoring. Our second objective was identifying the mismatches between the available methods and the current practices. Our third objective was to identify methodological issues specific to plants that will need further research to improve the accuracy and effectiveness of plant population monitoring programmes. Although much of what is presented in this review is valid regardless of the size of the studied species, we focus mainly on herbaceous plant species and have not presented the methods specific to the monitoring of trees.

Glossary

Demographic parameter : a measure of a demographic process, usually expressed relative to a time unit, such as the annual survival probability or recruitment rate. Also called 'vital rates'.

Imperfect detection : failure to detect all species or individuals during observation.

Judgement sampling : selecting the sample with some intention, for example, because it is thought to be representative of the population based on current knowledge, or for convenience reasons, such as to limit travel distance (YOCCOZ et al., 2001).

Metric : a type of measure that can be observed in the field, such as the number of individuals or the cover rate in a spatial unit.

Observation error : the difference between the observed and the true value of the variable of interest for a given sampling unit.

Probability sampling : selecting the sample based on randomness, with each sampling unit having a known positive selection probability.

State variable : variable within the system of interest used to characterise the

system status (YOCCOZ et al., 2001).

Statistical individual : the sample units composing the statistical population.

Statistical population : the entire set of sampling units to which survey findings are to be extrapolated (YOCCOZ et al., 2001).

Statistical power : the ability of a statistical procedure to distinguish a situation from the null hypothesis (GERRODETTE, 1987).

1.2 Population-level monitoring

Population-level monitoring refers to any study aiming to estimate the trend over time of a state variable characterising a biological population, such as the mean density of individuals or the mean cover rate, without tagging each biological individual observed in the field with an individual identifier. Therefore, the **STATISTICAL INDIVIDUALS*** are spatial units like quadrats or sites. The statistical population is the set of all possible spatial units, for example, all the quadrats covering a study area. As the fate of biological individuals is not tracked, the demographic mechanisms underlying the trend of the state variable remain unknown (WILLIAMS et al., 2002, p.333). Below, we first describe how to build the sampling design depending on the objective of the monitoring programme and the characteristics of the studied population, and then how to take into account observation errors depending on the state variable of interest.

1.2.1 Sampling design

The sampling process follows three steps : (1) define the statistical population ; (2) select a sample of spatial units from the statistical population using a given probability sampling method ; (3) estimate the state variable of interest and the associated uncertainty from the observations (COCHRAN, 1977). To estimate a trend over time, either a new sample is drawn at each occasion, or the units of the original sample are re-observed. Since many biological populations fluctuate over time non-monotonically, several sampling occasions are needed to reliably estimate the background trend of the state variable (DUCHENNE et al., 2022).

The statistical population can be defined according to biological criteria, such as a

species' distribution area, or arbitrary criteria, such as administrative or management boundaries. We will not further discuss how to define the statistical population because it is an organisational rather than a methodological issue. The statistical population has to be defined following a clear question, or a monitoring programme is unlikely to meet its objectives (NICHOLS & WILLIAMS, 2006). Once the statistical population is defined, three aspects determine the statistical power that a monitoring programme will achieve : (1) which sampling method is used to select the sample of spatial units, (2) how many sampling units are measured in total and (3) how this effort is allocated between spatial and temporal replication. This last point implies a trade-off between the number of sampling units and the number of time steps and depends on whether the same units are re-observed over time or whether a new sample is drawn at each time step.

1.2.1.1 Which spatial sampling method ?

When monitoring plant populations, especially for rare and aggregated species, it may be tempting to monitor only sites with high abundances of individuals, for example, because it is thought that these sites strongly contribute to the overall population trend. Moreover, sites with high abundances are usually easier to detect and historically well known, and searching for additional sites that may harbour few individuals may seem a waste of time. Whatever the reason, selecting the sample of monitored sites based on abundance usually results in a systematic bias toward population decline detection or exaggeration (FOURNIER et al., 2019; PECHMANN et al., 1991). There are two reasons for this : (1) if abundance at each site is stable but fluctuates randomly over time, selecting the sites with the highest abundances at the first time step will, on average, produce an observed decline (PALMER, 1993); (2) if historically known sites are monitored without searching for new sites, local extinctions may be observed, but no new colonisation will ever be observed (SKELLY et al., 2003). To obtain unbiased trend estimates at the scale of the statistical population (i.e. all the sites where the species occurs) using data from sites with high abundances that have been historically monitored, it is necessary to know or to estimate the number of sites that were not historically monitored, and to monitor them to estimate the average trend at these sites (CALENGE et al., 2022). Instead, using probability sampling from the outset ensures that the trend

estimates will be unbiased.

Many different sampling methods exist, for instance, simple random sampling, in which the sampling units are randomly selected, or systematic sampling, in which the location of the first unit is randomly selected, and the others are arranged along a rectangular grid (COCHRAN, 1977). The choice of the sampling method has little influence on the precision of the temporal trend estimates if the same sampling units are revisited throughout the monitoring programme. Conversely, this choice has a major effect if a new sample is drawn at each time step because the precision of the trend estimate then depends on the precision of the state variable estimates at each time step (hereafter called "point estimates" to differentiate them from "trend estimates"; URQUHART, 2012). The precision of point estimates depends on the variance of the statistical population (i.e. more variable populations lead to less precise estimates) and the sample size (i.e. larger sample sizes lead to more precise estimates). The two main issues when sampling plant populations are the aggregation of individuals and spatial rarity.

In biological populations, individuals are usually not randomly distributed in space (LEGENDRE, 1993; LEVIN, 1992). For plant species, individuals tend to be aggregated (DAMGAARD & IRVINE, 2019; GREIG-SMITH, 1983) due to limited dispersal capacity and patchy habitats (LARA-ROMERO et al., 2016; SEABLOOM et al., 2005). When sampling populations with aggregated individuals, samples typically have many zeros and a few high values, leading to a large sampling variance and imprecise estimates (MCGARVEY et al., 2016). However, the values of the sampling units are not randomly distributed in space as there is spatial dependence between them, i.e. the values of neighbouring units are positively correlated, which can be exploited to increase the precision of estimates (LAROCHE, 2022).

Increasing precision of point estimates for aggregated populations can be achieved by using sampling methods selecting units evenly distributed over the study area, such as systematic sampling or spatially balanced sampling (KERMORVANT et al., 2019), rather than random sampling. These methods never yield less precise estimates than random sampling for aggregated populations and can sometimes provide up to a 60-80% reduction of the sampling variance (MCGARVEY et al., 2016; PERRET et al., 2022). To improve the precision of these methods, the sampling design has to be tailored

to the aggregation of the population (see KERMORVANT et al., 2020; PERRET et al., 2022). However, due to the more even distribution of units, systematic and spatially balanced sampling have the disadvantage of causing larger travel distances than random sampling.

Adaptive Cluster Sampling (ACS; THOMPSON, 1990) can also increase the precision of point estimates. ACS is a two-step sampling method in which a sample of primary units is selected (usually through random sampling) and surveyed in the field. For the primary units satisfying a certain condition (e.g. the species is present, or the variable of interest exceeds a certain value), adjacent units are surveyed. This is repeated until no new units satisfying the condition are encountered. ACS usually increases the precision of estimates compared to random sampling for populations exhibiting aggregation (TURK & BORKOWSKI, 2005), with less total travel distance than non-adaptive sampling methods, as many adjacent units are surveyed. However, ACS has several drawbacks compared to non-adaptive sampling methods. First, the final sample size is only known once the sampling is complete, which can cause organisational and budget problems. Second, the precision gain depends on the spatial distribution of the variable of interest. ACS usually yields more precise estimates than one-step sampling methods if the sampling units satisfying the condition of interest form tight clusters and if there are enough clusters in the study area (or enough primary units are drawn) so that several clusters are intercepted by the primary units (PHILIPPI, 2005). If the clusters cover large areas, ACS usually provides no substantial precision gain compared to one-step sampling methods (MORRISON et al., 2008). If clusters are rare or cover small areas, ACS can lead to imprecise estimates (SHACKLETON et al., 2020). For an in-depth discussion about the conditions under which ACS is more efficient than other designs, see TURK et BORKOWSKI (2005). Given the logistical constraints associated with ACS and the uncertain advantage, we recommend using ACS rather than systematic or spatially balanced sampling only if the spatial distribution of the variable of interest is sufficiently known to be certain that it will be advantageous or if travel distance is very costly.

The spatial rarity of a species can arise from several different processes, leading to different forms of rarity and affecting which sampling strategy will be the most effective (KALTON & ANDERSON, 1986). In her seminal paper, RABINOWITZ (1981) proposed

a typology with seven categories of rare species based on the combinations of three criteria : geographic range (large or small), habitat specificity (wide or narrow ecological niche) and local abundance (large or small). For species with a wide ecological niche which are always locally sparse, the statistical population will typically be composed of many zeros (i.e. sampling units where the species is absent), and the units where the species is present will be approximately randomly distributed in space. In this case, all sampling designs will provide broadly the same precision of estimates, and the only way to get more precise estimates is to increase the sample size. On the contrary, for species with a narrow ecological niche, it is possible to increase the precision of estimates by stratifying the statistical population according to the ecological niche, for example, by creating two strata, favourable and unfavourable habitats, which will be sampled independently (COCHRAN, 1977, p.89). If there is a noticeable difference in the mean value of the variable of interest between the two strata, the estimate at the level of the statistical population will be more precise than if sampling was done without stratification (COCHRAN, 1977, p.100). If the ecological niche of the species is not well known prior to the monitoring programme, as it can happen for rare species, Adaptive Niche-Based Sampling (ANBS) can be used to estimate its ecological niche (GUISAN et al., 2006). In ANBS, existent data on the species are used to model its niche, new data are sampled by prioritising the favourable areas identified by the model, and the model is updated with the new data. Applying this process repeatedly improves the initial model at each iteration (CHIFFARD et al., 2020). Once the species' ecological niche is well identified, well-contrasted strata can be defined to get precise point estimates of the state variable of interest.

1.2.1.2 What temporal replication ?

The two most common types of temporal replication are to draw a sample at the first step and always revisit the same units or draw a new sample at each time step. In the first case, the precision of the mean trend estimate depends only on the level of temporal and spatial variation of the trend, i.e. how much the trend varies between spatial units and years relative to the 'background' trend. In the second case, the precision of the mean trend estimate depends additionally on the spatial variance of the variable of interest, i.e. the more its values vary in space, the less precise the mean trend estimate will

be. Thus, always revisiting the same spatial units provides more precise trend estimates than drawing a new sample at each time step (URQUHART, 2012). However, always revisiting the same units may carry the risk of impacting them through trampling, and it provides less precise point estimates than drawing new samples at each time step because fewer units are sampled. Precise point estimates may be of interest for a monitoring programme in addition to trend estimates, for instance, to assess the risk of the population falling below a minimum viable population size threshold (PIERCE et al., 2018). Panel plans, also called rotating panel plans, can be used to limit the negative impact of visits and obtain more precise point estimates than by always revisiting the same units. In panel plans, some units are revisited at each time step, and others are revisited less frequently (e.g. ten sites are visited annually, and five groups of 50 sites are visited every sixth year). Panel plans provide much more precise point estimates because more units are visited in total while providing almost as precise trend estimates as if the same units are always revisited (URQUHART, 2012).

Once the type of temporal replication has been chosen, it is necessary to decide how to allocate the sampling effort between space (i.e. increase the number of spatial units observed at each time step) and time (i.e. increase the frequency of revisitation). For the case where the same sites are always revisited, RHODES et JONZEN (2011) showed that the strategy to obtain the most precise trend estimates depends on the total sampling effort that will be engaged and five characteristics of the studied population : the trend's spatial autocorrelation (i.e. the level of correlation of the trend between neighbouring units), the trend's temporal autocorrelation (i.e. the level of correlation of the change between two time steps for the same spatial unit), the stochastic variation of the trend both in space and time (i.e. the level of "noise" in the trend), the spatial variation of the trend (e.g. if the background trend changes between favourable and unfavourable sites) and the presence of observation errors (if these are not modelled). If the trend's spatial correlation is high relative to the temporal correlation, the best strategy is to preferentially allocate sampling effort to temporal replicates, especially if observation errors and spatial variation of the temporal trend are low and/or the total sampling effort is large. Conversely, suppose the trend's spatial correlation is low relative to the temporal correlation. In that case, the best strategy is to preferentially allocate sampling effort to spatial replicates, especially if observation errors and the spatial variation of

the temporal trend are high and/or if the total sampling effort is small. These five population characteristics are seldom known before the start of a monitoring programme and have to be estimated with a pilot study to help choose the sampling design. If a pilot study is not possible, a rough assessment of the five population characteristics can be done based on what is known about the studied species. For example, for species with limited seed dispersal, the trend in the density of individuals will likely exhibit strong spatial autocorrelation as more seeds fall near areas where many individuals are already present (LARA-ROMERO et al., 2016). Furthermore, if the species is known for exhibiting density-dependent population growth rates, i.e. the density of individuals in a spatial unit positively or negatively affects the recruitment of new individuals in this unit, the trend in abundance will likely show strong temporal autocorrelation (GUNTON & KUNIN, 2009).

1.2.1.3 What total sampling effort ?

Increasing sampling effort improves the precision of trend estimates, or formulated from the perspective of statistical power, allowing weaker trends to be distinguished from the null hypothesis that the value of the state variable does not change over time. The population characteristics listed in the two sections above (e.g. spatial aggregation, the trend's spatial and temporal autocorrelation, etc.) determine the power that spatial sampling methods and temporal replication plans will achieve to detect a given trend. However, two other criteria are crucial for the statistical power of trend detection : the trend magnitude, i.e. weaker trends are harder to detect (LEGG & NAGY, 2006), and the timespan after which the trend is to be detected, i.e. trends are easier to detect over long periods than over short periods (WAUCHOPE et al., 2019; WHITE, 2019). For example, a monitoring programme whose objective is to be able to detect a decline in the density of individuals of 3% per year after ten years will require much more sampling effort than if the objective is to detect a 10% decline. Conversely, a 3% annual decline will require much less sampling effort to be detected after 20 years than ten years.

The only way to estimate the sample size needed to detect a given trend over a given period is to conduct a pilot study and complete a statistical power analysis (GERRODETTE, 1987). In a power analysis, the data collected during the pilot study are used to estimate the population characteristics influencing statistical power (e.g. spatial

and temporal variation in the trend, etc.). Next, these values are used to simulate populations subject to a trend of the magnitude to be detected. Monitoring programmes with various sampling efforts are then applied to the simulated populations, and the statistical power is computed as the proportion of simulations in which a statistically significant trend was successfully detected. Historically, conducting a power analysis required skills in statistics and much computational time, but many easy-to-use and efficient software are now available (e.g. WEISER et al., 2021).

TABLE 1.1 – Overview of the most commonly used methods for monitoring populations that allow correcting for imperfect detection. The column 'main constraints' concerns the methods in their simplest form and are often the consequence of the constitutive assumptions of the statistical models. Many statistical developments not presented here have allowed for the loosening of certain assumptions, thus mitigating some of the stated constraints.

State variable	Metric	Statistical model	Advantages over other models for estimating the same state variable	Main constraints	Reference publication(s)
Demographic parameters	Presence-absence of marked individuals at each capture occasion	Open population mark-recapture model	Detection probability can be different between marked and unmarked individuals.	Requires to repeat captures over multiple seasons and to use marks lasting the entire study duration; Very labour-intensive, which usually limits sample size and may lead to limited extrapolation capacity.	Cormack (1964) and Lebreton et al. (1992)
Density of individuals	Presence-absence of marked individuals at each capture occasion	Jolly-Seber model	Allows to estimate both population size and survival probability.	Requires to repeat captures over multiple seasons and to use marks lasting the entire study duration; Marked and unmarked individuals need to have the same detection probability.	Jolly (1965) and Seber (1965)

State variable	Metric	Statistical model	Advantages over other models for estimating the same state variable	Main constraints	Reference publication(s)
Density of individuals	Presence-absence of marked individuals at each capture occasion	Closed population mark-recapture model	Marks need to last only one season; Provide more precise estimates than N-mixture models.	Requires to repeat captures within the same season and to use marks lasting one season; Population has to be closed within each season.	Otis et al. (1978)
Density of individuals	Number of individuals	N-mixture	Does not require to mark individuals	Requires to revisit sites within the same season; Sites have to be closed within each season; Parameter estimation is unstable when counts are highly variable.	Royle (2004)
Density of individuals	Distances between the observer and the detected individuals	Distance sampling	Does not require multiple visits; Practical to implement for large study areas.	Species have to be easy to detect at short distance; Difficult to use if densities of individuals are high.	Burnham and Anderson (1976)
Cover rate	Cover rate	Zero-augmented beta with observation errors (ZABE) model		Requires to revisit sites within the same season.	Wright et al. (2017) for ZABE; Irvine et al. (2019) for extension of the model to cover classes analysis (OZABE)

State variable	va-	Metric	Statistical model	Advantages over other models for estimating the same state variable	Main constraints	Reference publication(s)
Site occupancy		Presence-absence of the species	Detection/non-detection occupancy model		Requires to revisit sites within the same season; Site's occupancy status has to be constant within each season.	MacKenzie et al. (2002) and Tyre et al. (2003) for single season models; MacKenzie et al. (2003) for multi-season models
Site occupancy		Time until the species is detected	Time-to-detection occupancy model	Does not require multiple visits; More precise estimates than site occupancy models with the same number of visits.	Site's occupancy status has to be constant within each season.	Garrard et al. (2008)

1.2.2 Observation process and analysis

For plants, the three main state variables studied at the population level are site occupancy probability, individual density and cover rate. Site occupancy probability refers to the probability that a species occupies a spatial unit. The spatial units can be ecological entities such as ponds (MACKENZIE et al., 2003) or cells exhaustively covering a study area (LOUVRIER et al., 2018). The density of individuals is the mean number of individuals per unit area across the statistical population. The population size is calculated by multiplying the mean density estimate by the total area of the statistical population. The cover rate refers to the proportion of area a species covers when all parts of all individuals are projected onto the ground surface. In plant studies, the density of individuals and the cover rate are sometimes referred to as "species abundance"; therefore, to avoid ambiguity we will not use this term.

For site occupancy probability and density of individuals, the main observation error leading to biased estimates is imperfect detection. Indeed, imperfect detection is the rule rather than the exception for plants when searching for a species or individuals. The detection probability varies depending on observational and ecological variables (CHEN et al., 2013; PERRET et al., 2023); it increases with survey effort (CHEN et al., 2009) and often varies between observers (GARRARD et al., 2008; MOORE et al., 2011). Detection also varies with the morphology of the target species (CHEN et al., 2013; CHEN et al., 2009; GARRARD et al., 2013; HAUSER et al., 2022), with conspicuous growth forms and phenological stages being more detected, while the closure of the habitat decreases detection probability (GARRARD et al., 2008; PERRET et al., 2023). Higher densities of individuals in a spatial unit increase the probability of detecting the species (BORNAND et al., 2014) but decrease the probability of detecting individuals (PERRET et al., 2023). For cover rate, there are two nested levels of observation error : not detecting that the species is present in a spatial unit and making an estimation error when visually estimating the area covered by the species (WRIGHT et al., 2017).

Multiple methods have been developed for estimating these observation errors and thus getting unbiased estimates (Table 1). Each method makes it possible to estimate a given state variable (e.g. density of individuals) based on a specific metric (e.g. counts of individuals) and a specific procedure for taking the field measurements (e.g. carrying out independent repeated counts in each spatial unit), while explicitly modelling the observation process. In addition to estimating the temporal trend of the state variable, these methods also allow getting the point estimates of the state variable at each time step of the monitoring programme and estimate the effect of covariates on the detection probability and the state variable (e.g. estimating the effect of the habitat on the detection of individuals or the density of individuals).

1.2.2.1 Estimating site occupancy

The first way to estimate occupancy probability while correcting for imperfect detection is to use the Detection/Non-Detection model, hereafter called 'DND' (MACKENZIE et al., 2002; TYRE et al., 2003). With this method, a sample of spatial units (usually called sites in studies using DND) has to be surveyed multiple times with a similar survey effort (e.g. a fixed survey time). The revisits must be independent, i.e. the observers

must not remember where the individuals were on the previous visit, and close enough in time so that the occupation status of the sites does not change, i.e. occupied sites remain occupied and unoccupied sites remain unoccupied. For each site in the sample, a detection history is collected as a series of zeroes (the species was not detected on this visit) and ones (the species was detected). Then, the detection and occupancy probabilities are jointly estimated from these detection histories by maximum likelihood (see BOLKER, 2008, for an introduction to maximum likelihood estimation). Intuitively, if, for sites where the species has been detected at least once, the detection histories are composed mostly of ones, the detection probability is high since the species is rarely missed where it is present.

Conversely, if detection histories are composed of many zeros and a few ones, the detection probability is low, as the species is seldom detected in occupied sites. The DND method quickly became very popular (Box 1), and many methodological developments have been made to adapt it to complex situations. For instance, it is possible to consider species identification errors that lead to false positives (ROYLE & LINK, 2006), estimate detection probability from repeated visits on a subset of sites, and correct for imperfect detection over all the surveyed sites (MACKENZIE & ROYLE, 2005). In addition, most methodological developments are available in the open source R package 'unmarked' (CHANDLER et al., 2022). The main limitation of using the DND method for plants is the hypothesis of visit independence, which is unlikely to be respected if the same observer does repeated visits due to plants' sessile nature. To avoid biased estimates due to memory effects, either each visit to a site has to be made by a different observer, or the number of visits to a site has to be added to the model as a covariate to estimate its effect on the detection probability (MACKENZIE et al., 2017).

The second way to estimate occupancy probability is the Time-To-Detection (TTD) method (GARRARD et al., 2008). With this method, a maximum survey time is chosen and a sample of sites is surveyed. For each visit, the time until the species is detected is recorded, and a zero is recorded if the species is not detected after the maximum survey time. The time-dependent species detection probability and the occupancy probability are jointly estimated from the recorded times to detection. The main advantage of TTD over the DND method is that it is possible to estimate the detection probability with a

single visit per site (GARRARD et al., 2008). The relative performance of single-visit TTD compared to multiple-visit DND in terms of occupancy probability estimate precision depends on how widespread and hard to detect the studied species is. However, for the same number of visits and maximum survey time per site, TTD always outperforms the DND method (BORNAND et al., 2014; HENRY et al., 2020).

There are two ways to estimate a temporal trend in occupancy probability. A separate DND or TTD model can be fitted to each year's data, or a multi-season model can be fitted to all years' data. In a multi-season model, four probabilities are jointly estimated : the detection probability, the occupancy probability at the first time step, the probability of an unoccupied site to be colonised by the species between two seasons, and the probability of the species becoming extinct at a site between two seasons (MACKENZIE et al., 2003). Multi-season models benefit from the sharing of information between years, which increases the precision of estimates, and that the correlation between site colonisation and extinction probabilities and ecological variables can be tested, allowing insight into what determines the species' spatial dynamics.

1.2.2.2 Estimating density of individuals

The first way to estimate the density of individuals without bias is to use the N-mixture method (ROYLE, 2004). With this method, repeated counts of individuals are carried out on a sample of spatial units. The detection probability of individuals and the number of individuals in each spatial unit are jointly estimated from the repeated counts using maximum likelihood. Similarly to the methods for estimating occupancy probability, the repeated counts must be independent, and the number of individuals in each site must be constant during the revisits. In addition, all individuals must have a similar detection probability, which can be problematic for plants as it is common for flowering and non-flowering individuals to be present simultaneously in a population. However, N-mixture models are robust to the violation of this hypothesis as long as individual detection probabilities are high (typically above 0.5, see VEECH et al., 2016). As for the methods for estimating occupancy probability, the detection probability can be estimated from repeated counts on a subset of spatial units. Temporal trends in the density of individuals can be estimated either by fitting a separate N-mixture model to the data of each year or by fitting a single dynamic N-mixture model to the data of all

years (KÉRY et al., 2009). In dynamic N-mixture models, the number of individuals at the first survey year and an annual population growth rate are estimated for each site in addition to the individual detection probability. These models allow to test the effect of covariates on the density of individuals and its variation over time, e.g. test the effect of site characteristics on the local population growth rate.

The second way to obtain unbiased estimates of the density of individuals is to use the distance sampling method (BUCKLAND et al., 1993), where line transects are placed across the study area following some distribution (e.g. random, systematic). An observer follows each transect, and whenever he observes an individual, he measures the distance between the individual and the transect line. By supposing that the detection probability of individuals decreases with the distance from the transect line, the distribution of the observed distances is used to estimate a "detection function" that describes the probability of detecting an individual at a given distance. Once this function is estimated, the density of individuals can be estimated using the number of individuals detected during the surveys. The main advantage of distance sampling is that detection probability can be estimated from a single visit. This method has been successfully used for plants to estimate densities of individuals of conspicuous species occurring at low densities over wide study areas (e.g. CHARPENTIER et al., 2020). However, due to the time needed to measure the distance to the detected individuals, distance sampling is impractical to study species of small herbaceous plants occurring at high density. Several ways have been developed to estimate temporal trends from distance sampling data described in THOMAS et al. (2004).

The two methods presented above estimate the density of individuals based on counts or distances between the observer and detected individuals. Other methods have been developed to estimate the density of individuals based on metrics whose relationship with density is less direct. For instance, in the method proposed by ROYLE et NICHOLS (2003), repeated visits are made on spatial units, and species detection histories are collected, exactly as for the DND method to estimate occupancy probability. However, the hypothesis is taken that the density of individuals is the main variable explaining the heterogeneity of the species detection probability between spatial units. Under this hypothesis, it is possible to estimate the number of individuals in each spatial

unit from the difference in estimated detection probability between the spatial units.

Similarly, STREBEL et al. (2021) developed a method called TTD-N-mixture that allows to estimate the density of individuals from single or repeated measurements of species time-to-detection. To our knowledge, these two methods have never been used on plants yet. They are probably impractical for species occurring at high densities that are typically studied using small quadrats (e.g. 1x1 m). However, they could be useful for rare and inconspicuous species typically searched in big spatial units (e.g. 20x20 m or 100x100 m quadrats). However, both the Royle-Nichols method and the method developed by STREBEL et al. (2021) rely on strong assumptions about the link between detection probability and the density of individuals, which need to be carefully checked in the context of plant studies.

1.2.2.3 Estimating cover rate

Cover rate is a state variable specific to sessile life forms, including plants and sessile animals such as mussels and other intertidal species (SAGARIN & GAINES, 2002). For plants, the use of cover rate has a long history in community ecology, where it is used to measure the relative abundance of species (BRAUN-BLANQUET, 1964). In studies on plant populations, the cover rate is usually used as a proxy for the density of individuals. The cover rate can be measured with multiple field methods, the most common being visually estimating the area covered by a species in spatial units, usually small quadrats. In addition, the cover rate is often measured on an ordinal scale of classes instead of net measures (e.g. <0.01, 0.01-0.05, 0.05-0.25, 0.25-0.5, 0.5-0.75, 0.75-1). Several scales exist (for a synthesis of field methods and measurement scales, see DAMGAARD & IRVINE, 2019). While the visual estimation of cover rate is quick to measure in the field, it is highly variable between observers (HAHN & SCHEURING, 2003; MILBERG et al., 2008; VITTOZ et al., 2010), and even for observers repeating measurements on the same spatial units (SYKES et al., 1983). Thus, cover rate measurements are subject to two nested errors : not detecting the species in a spatial unit and inaccurately estimating the area covered by the detected individuals (MILBERG et al., 2008). Both error probabilities need to be estimated to obtain unbiased estimates of the mean cover rate over a given study area.

Methods for modelling the observation process for visual estimations of cover rate are extensions of the N-mixture method for counts : observers have to carry out independent repeated measurements on a sample of spatial units, and a statistical model fitted to the resulting data is used to jointly estimate both error probabilities. The first model developed for this objective is the Zero-augmented beta error model (ZABE; WRIGHT et al., 2017). The ZABE model takes as input net cover rates and estimates four parameters : the species detection and occupancy probabilities, the visual cover assessment error rate, and the mean cover rate. Using simulations, the developers of this model showed that the ZABE model provides unbiased estimates of the mean cover rate. In contrast, the estimates obtained with other models not accounting for imperfect detection and visual assessment errors yield systematically biased estimates (WRIGHT et al., 2017). The second methodological development was extending the ZABE model to take ordinal cover classes as input data (IRVINE et al., 2019). The resulting model, OZABE, works on the same principle, but the mean cover rate is modelled as a latent partially observed variable. OZABE provides unbiased estimates under favourable conditions, but the model sometimes fails to converge for species with low occupancy probability or detection probability, while the ZABE model does not suffer these drawbacks. ZABE and OZABE are very promising methodological developments for estimating cover rates, and proofs of concept of their workability have been provided (e.g. RODHOUSE et al., 2020). However, their use requires large data sets, and convergence failure may occur for rare or inconspicuous species (IRVINE et al., 2019).

1.2.2.4 Estimating demographic parameters from the number of individuals per class

For plant species for which it is possible to identify individuals of different ages or life stages (e.g. seedling, vegetative individual, flowering individual), it is a common practice to estimate demographic parameters from repeated counts of unmarked individuals in each class without correcting for imperfect detection (Box 2). In this kind of method, the number of individuals per class is counted every year on fixed spatial units, such as quadrats randomly located across the study area. The fecundity rate is then estimated by dividing the number of seedlings at year $t+1$ by the number of flowering individuals at year t . The same logic is employed to estimate the survival probability of

individuals of each class (e.g. GILJOHANN et al., 2017; TREURNICHT et al., 2021). This way of estimating demographic parameters relies on two strong hypotheses : (1) that all individuals are detected or that the detection probability is identical for all classes of individuals, and (2) that there is no seed bank and that all individuals transit to the next class every year. Indeed, if some classes of individuals are less detected than others, and if seeds from previous years germinate or some individuals stay in the same class for multiple years, the demographic parameters estimates will be biased. Several studies on monitoring marked individuals have shown that these two hypotheses were false for multiple species. In these studies, the detection probability usually depended on the life stage, and the transition of individuals between stages was not systematic (ALEXANDER et al., 1997; ANDRIEU et al., 2017; KÉRY et al., 2005; KÉRY & GREGG, 2003). Thus, we recommend avoiding using this method unless there is strong evidence that the two above hypotheses will be respected.

1.2.3 Methodological perspectives and limitations of population-level monitoring

The above methods use a single metric from a single observation process to estimate population-level state variables. However, it is common that several types of data are collected on a population, which are usually analysed separately. Data integration involves integrating data from multiple observation processes into the same statistical model. The principle is to use the information from multiple data sources, such as studies made for different purposes, to get more precise estimates than if each data type was analysed separately (ISAAC et al., 2020). For example, repeated counts of individuals can be carried out on a sample of spatial units, and distance sampling can be carried out on line transects randomly located across the same study area. The density of individuals is then modelled as a latent variable observed with two observation processes : the N-mixture method and the distance sampling method (KÉRY et al., 2022). For plants, data integration is particularly promising for improving the precision of occupancy probability estimates because methods have been developed to integrate data collected according to a formalised protocol and opportunist species observations (called 'presence-only data'), which are often very abundant for plants (e.g. KOSHKINA et al., 2017).

A major methodological issue specific to plants is that for some species, it is difficult, if not impossible, to differentiate individuals, for example, because of vegetative reproduction through stolons or because individuals grow close to each other and mix their stems (HARPER & WHITE, 1974). For some species, it is impossible to differentiate genets, i.e. genetically different individuals, but ramets, i.e. genetically identical individuals originating from asexual reproduction, may be differentiated. For these species, the density of ramets may be estimated using the methods described above, given that it is a biologically meaningful state variable for the studied species. For the species where genets cannot be differentiated, and no biologically meaningful ramets are available, the density of individuals is impossible to estimate.

In monitoring programmes for conservation, the objective is sometimes to obtain an indicator of a population's conservation status without being interested in a specific state variable. Thus, the choice of the state variable is not driven by a research question, and any state variable may be a candidate for monitoring (CARIGNAN & VILLARD, 2002). However, the relations between the possible state variables for a given population are often unknown (e.g. what decline in the density of individuals is needed before a decline in occupancy happens); thus, extrapolating the results to the other state variables is not trivial. In addition, the relative performance of the different methods to detect a given trend in the corresponding state variable is currently unknown for plants. Depending on the study conditions, such as the species' conspicuousness, spatial rarity, and habitat closure, it is probably highly variable.

Box 1 : Cross-taxa history of imperfect detection modelling methods

Detection probability is far less frequently estimated for plants than for several animal taxa when estimating population-level state variables and demographic parameters (KELLNER & SWIHART, 2014). To understand the underlying process, we investigated for which taxa the methods allowing to estimate detection probability were first developed and how their use spread between taxa, including plants. For this purpose, we selected five methods to estimate the detection probability of species (Detection/Non-Detection and Time-to-detection site occupancy) or individuals (Distance sampling, Capture-Recapture for closed population, N-mixture). For each method, we identified a founding publication and

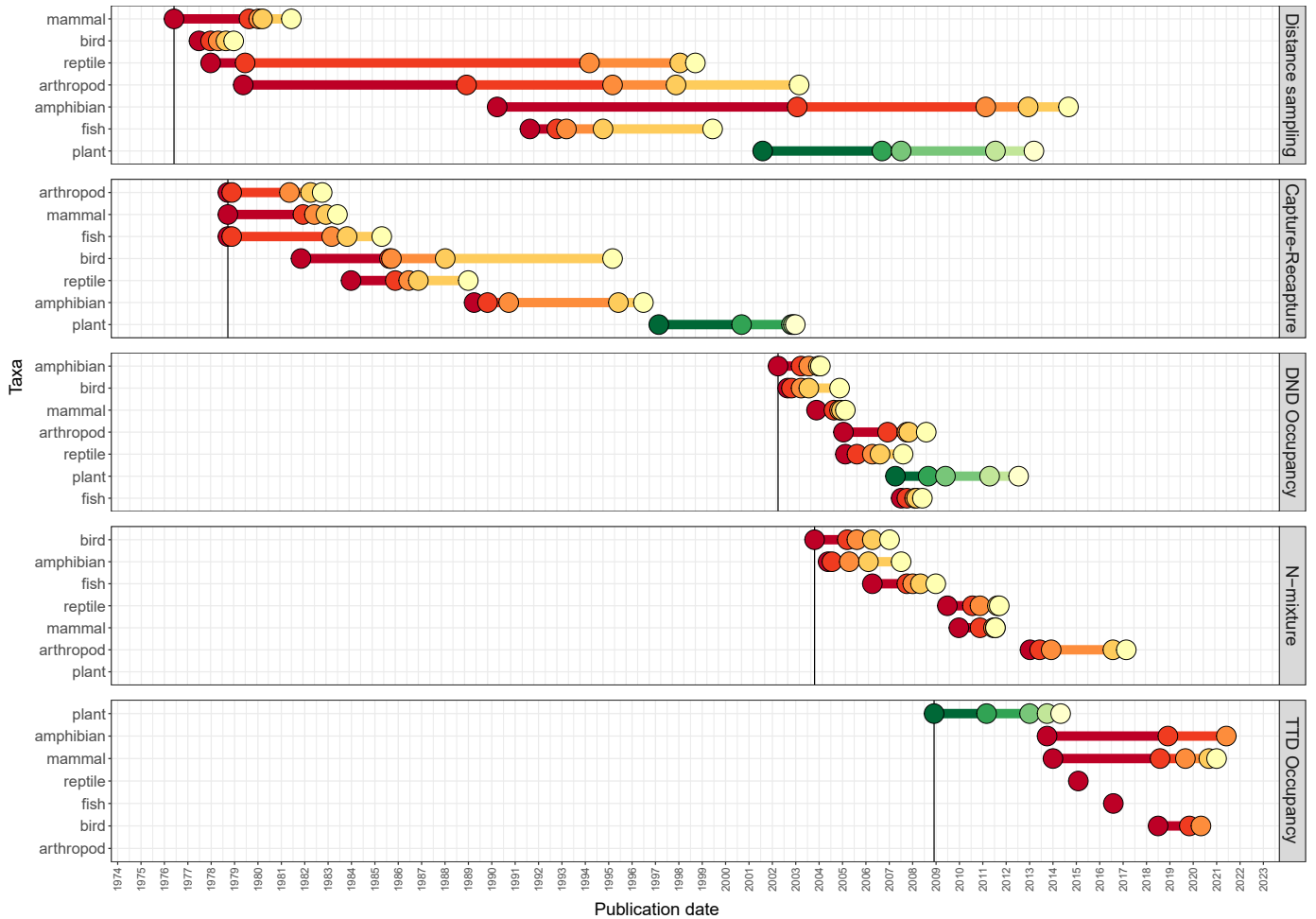


FIGURE 1.1 – Timeline showing the first five articles using five imperfect detection modelling methods (Distance sampling, Capture-Recapture for closed population, Detection/Non-Detection (DND) occupancy, N-mixture and Time-to-detection (TTD) site occupancy) for seven taxa (amphibians, arthropods, birds, fishes, mammals, plants and reptiles). The vertical black lines represent the founding publication of each method and the circles represent the articles, with the green representing plants

searched several online databases for the first five articles that used the method for each of the seven taxa (five vertebrate taxa, arthropods and plants). How we searched the articles is detailed in Appendix 1, and the results are shown in Figure 1.1.

Four of the five methods were applied to animal taxa first, and plants were the last or second-to-last taxa to which they were applied. The time lag between the publication of the method's founding article and the first article using it on plants was 25 years for Distance sampling and 19 years for closed population Capture-Recapture. The founding article for the N-mixture method was published 19 years ago, and to date, no article using it on plants has been published. The situation is different for the Detection/Non-Detection site occupancy method, for which only five years separate the founding publication from the first article using it on plants, even though it was shorter for most other taxa. The situation is reversed for the Time-to-detection method : it was first applied to plants and later diffused to animal taxa.

1.3 Individual monitoring

Individual monitoring refers to studies in which biological individuals observed in the field are marked with individual identifiers, which allows following their fate over time. Individual monitoring aims to estimate the population size at a given time or to estimate demographic parameters such as survival, recruitment and transitions between life stages. For individual monitoring, the statistical individuals are biological individuals (i.e. for plants, whether genets or ramets), and the statistical population is the set of all the individuals constituting the biological population. As the detection of individuals is usually imperfect, their detection probability has to be estimated to get unbiased estimates of population size or demographic parameters (ALEXANDER et al., 1997; KÉRY & GREGG, 2003). This is done through 'Capture-Recapture' methods (hereafter CR), which require repeated capture occasions during which all the detected individuals are recorded so that the detection history of each individual is known. The CR methods were historically developed for vertebrates, and the capture occasions were typically days of trapping. For sessile organisms such as plants, the capture occasions

are more properly called 'detection occasions' and consist of repeated visits to spatial units, such as quadrats or sites. In the sections below, we describe how to build the sampling design of an individual monitoring study and how to get unbiased estimates of population size and demographic parameters by estimating the detection probability of individuals with the CR methods.

1.3.1 Sampling design

For studies aimed at estimating population size, the considerations related to the sampling design are identical to those for population-level monitoring. Carrying out repeated visits on spatial units and marking the detected individuals allows to estimate the detection probability of individuals and obtain unbiased estimates of the number of individuals in each spatial unit, but the issue of spatial variation remains. Thus, the same guidelines as for population-level monitoring studies remain valid concerning spatial sampling to get more precise point estimates (section 1.2.1.1), temporal replication to get more precise trend estimates (section 1.2.1.2) and total sampling effort to meet the study's objectives (section 1.2.1.3). The situation is different for studies aimed at estimating demographic parameters. Concerning temporal replication, relying on fixed spatial units for sessile organisms is unavoidable since demographic parameters cannot be estimated if the detected individuals cannot be re-observed over time, which would be the case if a new sample of spatial units is drawn at each time step. The main issue regarding sampling is the representativeness of the monitored individuals. For example, suppose the spatial units are located only on the margin of a study site where the habitat is less favourable. In that case, estimates of survival probability may be underestimated compared to the value for the entire population. As for population-level monitoring, spatial units should be selected with probability sampling methods, and judgement sampling should be avoided (WILLIAMS et al., 2002, p.489). The issue of sample representativeness (FLETCHER et al., 2012) is rarely discussed in individual monitoring studies, and, commonly, the method to select spatial units is not clearly explained (but see, e.g., ANDRELLO et al., 2012). The precision of demographic parameter estimates depends on the number of monitored individuals and the number of transitions between states that are observed (e.g. living to dead for survival probability, vegetative to flowering for flowering probability.). In plant individual monitoring studies, it is common to mo-

nitor individuals in a single spatial unit, either a site defined on ecological criteria or a unique large quadrat (ALEXANDER et al., 1997; KÉRY & GREGG, 2003). With this design, the inference is limited to the monitored individuals and the results cannot be extrapolated over a larger study area, as demographic parameters might be subject to spatial variation.

1.3.2 Observation process and analysis

1.3.2.1 Estimating population size

Estimating population size by marking individuals is done through 'closed population capture-recapture', which relies on the hypothesis that the studied population is closed while the visits are carried out, i.e. the population does not gain or lose individuals (OTIS et al., 1978). In closed population CR, repeated visits are carried out on spatial units, and all detected biological individuals are marked. The marking has to last for the duration of the detection occasions and does not need to be permanent. For instance, hanging a plastic tag on the stem of each detected individual or writing a number on a leaf with a permanent marker is sufficient if the detection occasions are on successive days. On each detection occasion, all previously detected individuals are recorded, and individuals detected for the first time are marked so the detection history of each individual is known. For example, if three visits are carried out on a site, an individual detected only on the second occasion will have the detection history 010, and an individual detected on the two first occasions but not on the third will have the history 110. To estimate the detection probability and the number of individuals from these detection histories, three hypotheses are taken : (1) the population is closed, (2) individuals do not lose their marks during the timespan of the study, and the observer correctly records marks, and (3) all individuals have a constant and equal detection probability (OTIS et al., 1978). Under these hypotheses, the detection probability and the number of individuals are jointly estimated from the detection histories of individuals by maximum likelihood. Intuitively, the proportion of zeros in detection histories allows to estimate the detection probability, as all individuals detected at least once are still in the population (closure hypothesis). The number of individuals can be estimated using the detection probability, the number of detection occasions and the total number

of detected individuals.

Hypotheses 1 (population closure) and 2 (no tag loss or recording errors) can be assured by a careful study design, field tests and appropriate training of workers. However, hypothesis 3 (constant and equal detection for all individuals) is unlikely to be met in most plant studies. For instance, the detection probability of plant individuals depends on the phenological state, e.g. seedlings are less detected than flowering individuals (ALEXANDER et al., 1997; ANDRIEU et al., 2017), and marked individuals are more detected than unmarked ones (KÉRY & GREGG, 2003). However, many methodological developments have been made for relaxing this hypothesis, synthesised in the seminal paper by OTIS et al. (1978). They proposed eight models allowing unbiased estimation in the case of detection probability varying between marked and unmarked individuals, varying between detection occasions, varying between individuals, and combinations of these three types of unequal detection probability. These developments have made closed-population CR flexible and usable in many field situations.

1.3.2.2 Estimating demographic parameters

Estimating demographic parameters requires monitoring the fate of individuals through time, typically during several years for perennial plant species. Repeated visits on spatial units have to be carried out, during which all detected individuals are recorded, and individuals detected for the first time are marked using permanent marks. Several types of marks can be used for plants, such as gardening labels planted next to each detected plant and numbered tags placed around stems (e.g. JIMÉNEZ-ALFARO & IRIONDO, 2014; KÉRY & GREGG, 2003). Another method is to precisely locate each individual in a fixed quadrat, so if an individual is later detected at the same position, it is certainly the same individual (e.g. ALEXANDER et al., 1997). This method avoids the use of physical tags, which may be lost, but requires the coordinates of the individuals to be more precise than the minimum distance between individuals, which is unsuitable for dense populations. The demographic parameters of interest in plant individual monitoring studies are usually survival probability (often by life-state), recruitment rate and transition probabilities between life-states (e.g. probability of a seedling becoming a mature vegetative individual, of a vegetative individual to enter anthesis, etc.). If the detection of individuals was perfect, these probabilities could be estimated by computing

the proportion of individuals making each state transition every year, i.e. the proportion of vegetative individuals that died, the proportion of vegetative individuals entering anthesis, etc. However, due to imperfect detection, an unobserved individual may be dead, living but dormant or living but missed by the observer. In addition, inconspicuous individuals will be less detected, leading to samples of monitored individuals biased towards conspicuous life-states and taller individuals. Estimating demographic parameters without accounting for imperfect detection generates many issues : biased estimates of survival and state-transition probabilities, spurious relationships between demographic parameters and covariates, and underestimated recruitment rates (for a detailed synthesis, see KÉRY & GREGG, 2003).

The 'open population capture-recapture' methods use detection histories of individuals, but the detection occasions are more distant in time than for closed population CR, and no population closure hypothesis is made. For a study with one detection occasion every year, a typical detection history could be 0101100, i.e. the individual was first detected in the 2nd year and seen again in the fourth and fifth years. The fate of this individual after the 5th year is uncertain, as the zeros of the sixth and seventh years could either mean that the individual died between the fifth and sixth detection occasions or that it was living but undetected. To estimate the detection probability and demographic parameters despite this uncertainty, the probability of each possible detection history is expressed as functions of the model parameters, i.e. for the simplest case, as a function of detection, survival and recruitment probabilities. The parameter values are estimated by maximum likelihood based on the frequency of each detection history in the dataset and the functions linking each possible detection history to the model parameters (LEBRETON et al., 1992). The same principle is applied to estimate parameters of more complex models corresponding to species with complex life cycles, such as with transitions between multiple life-states, the possibility of dormancy or the possibility that seeds enter the seed bank instead of germinating immediately (ANDRIEU et al., 2017; KÉRY et al., 2005). If there is only one detection occasion each year, demographic parameters can be estimated, but not the population size, as there are no repeated visits during a time period where the population is closed. The 'robust design' (Pollock 1982) allows for estimating both the population size of each year and the demographic parameters by conducting multiple visits each year. The robust design combines the

advantages of closed and open population CR, as each year can be viewed as a closed population, and years are linked through an open population CR model. The robust design yields more precise parameter estimates than separated closed and open population CR models, and estimates are more robust to the departure of the model hypothesis (WILLIAMS et al., 2002).

1.3.3 Demographic prediction

To understand the dynamics of a population, the demographic parameters estimated with open population CR have to be combined into a population model, such as matrix models. These are mathematical tools used to describe the functioning of a population and not statistical models used to estimate parameters from field data. They take the form of matrices whose cells contain the transition probabilities between the states represented by each row and column. They allow to estimate the evolution of the number of individuals per state over a chosen time interval, to estimate the asymptotic growth rate of the population (i.e. the temporal trend of the population size), its extinction risk at a given time horizon, and the sensibility of the growth rate to modifications of the value of each demographic parameter. This allows to identify which parameter is the most critical to the population's fate, i.e. on which parameter conservation actions will be the most efficient to reduce extinction risks. Many methodological developments have been made on matrix models, such as modelling demographic and environmental stochasticity and density dependence on demographic parameters. For a complete synthesis of matrix models, see (CASWELL, 2001).

Matrix models require individuals to be classified into discrete stage classes. This may be meaningless for some plant species, as the variable with the most influence on survival and fecundity can be a continuous variable such as plant size or biomass. Integral projection models have been developed to avoid discretising a continuous variable into classes (EASTERLING et al., 2000). Integral projection models follow the same principles as matrix models. However, instead of state transition probabilities, they take three functions as input : 1/ the growth function describing how the chosen continuous variable (e.g. plant height) changes over time, 2/ the survival function describing how the continuous variable influences individual survival, and 3/ the fecundity function describing how fecundity depends on the continuous variable. The parame-

ters of these functions are estimated from individual-level monitoring data, where the chosen continuous variable is measured on each detected individual every time it is detected. Integral projection models allow to perform the same analysis as matrix models, such as estimating the asymptotic growth rate of the population and its sensitivity to changes in demographic parameters, i.e. the values of the parameters in the three functions. Integral projection models have also been extended to model dormant life stages, populations structured by multiple variables (e.g. size and age), and changes between discrete and continuous structures in the life cycle (ELLNER & REES, 2006).

1.3.4 Methodological perspectives and limitations of individual monitoring

Individual monitoring has limitations specific to plants that do not occur when studying vertebrates for which the CR and demographic projection methods were initially developed (Box 1 ; CASWELL, 2001 ; WILLIAMS et al., 2002). First, it is impossible for some species to delimit individuals with certainty. Second, for some species, it is impossible to mark individuals permanently. For instance, for geophytes, no type of tag can identify which individual was initially marked if two individuals emerge next to each other after a period of dormancy. Third, the density of individuals can be very high in plant populations, making it difficult, if not impossible, to tag individuals. Fourth, estimating demographic parameters for pioneer and annual plants is challenging, as the seed bank plays a central role and is usually impossible to observe (STOUFFER, 2022). These methodological issues are seldom addressed in the methodological literature, and most plant individual monitoring studies focus on species that do not present the four characteristics above (Box 2).

Box 2 : Profile of plant population monitoring studies published between 2010 and 2019

Our objective with this box was to establish the profile of the recently published plant population monitoring studies regarding state variables of interest, monitoring methods and studied species. For this purpose, we searched Web of Science for all the articles published between 2010 and 2019 containing the following words in their title, abstract or keywords : "population AND (monitoring OR de-

mography OR dynamic OR trend OR viability analysis)". We refined the result by keeping only articles published in five journals leading in plant ecology and conservation biology : *Biological Conservation*, *Conservation biology*, *Ecology*, *Journal of Applied Ecology* and *Journal of Ecology*. We used the text mining software 'gnfinder' (MOZZHERIN et al., 2022) on each article's title, abstract and keywords to find the name of the studied taxa. We kept only articles studying a single Tracheophyte species. The resulting corpus contained 201 articles. We read their abstracts and excluded the articles that were not properly population monitoring (e.g. if 'population monitoring' was mentioned in the abstract as a perspective) and those that were studying tree species. For the remaining articles, we extracted the state variable of interest, the metric and the statistical model used, and the study's timespan. In addition, we queried the plant trait database TRY (KATTGE et al., 2020) to get the lifespan (annual or perennial) and the Raunkiær life form (RAUNKIÆR, 1934) of each species in the corpus. The results are shown in Figure 1.2.

The corpus included 96 relevant articles not dealing with the monitoring of tree species (see Appendix 2 for a general description of the corpus, including the filtration steps). Most articles focused on demographic parameters ($n = 92$), a few on the density of individuals ($n = 13$), and two papers on occupancy probability. The metrics recorded in the field were counts of individuals on spatial units for studies focusing on the density of individuals and detections of the species for studies focusing on occupancy. Two metrics are commonly used to estimate demographic parameters : the presence or absence of marked individuals and counts of unmarked individuals in different age groups (e.g. the number of seedlings, vegetative and flowering individuals). We could not tell which metric was used from reading the abstract and keywords for most studies, so we did not report this information. Of the 96 relevant articles in the corpus, only three mentioned a method for estimating detection probability ; in all three cases, capture-recapture models. For most other studies, imperfect detection was likely not accounted for. If the authors had gone through the trouble of estimating detection probability, they would have said it explicitly, especially as it raises the methodological stan-

dard of their studies. Regarding the statistical models, most articles focusing on demographic parameters only mentioned matrix models or integral projection models, two models used to predict future population dynamics based on previously estimated demographic parameters. The mean timespan of the studies in the corpus was 11.2 years, ranging from 1.5 to 46 years. Most studied species were perennials; hemicryptophyte and geophyte were the most common life forms.

1.4 Discussion and perspectives

1.4.1 Comparing population-level and individual monitoring

Population-level monitoring is usually less labour-intensive than individual monitoring, which allows covering large study areas but does not allow to identify which demographic process drives an observed state variable trend. The only exception is estimating demographic parameters from counts of unmarked individuals per age class or life stage, but this method raises serious methodological concerns. For instance, a decline in the density of individuals may arise from less seedling recruitment or higher adult mortality, which may lead to different management actions in a conservation context. Therefore, the results of population-level monitoring can be of limited use to both ecological research and conservation biology, as both often require understanding the functioning of populations.

Individual monitoring allows to estimate demographic parameters. However, it is more labour-intensive than population-level monitoring, which limits the spatial extent of studies and can be difficult to implement for some plant species. Most population monitoring methods were initially developed to monitor populations of vertebrates. These methods are directly transposable for some plant species without further methodological developments. However, other species raise specific issues due to complex distribution patterns, complex life cycles and morphologies, making it impossible to delimit individuals. There is a dire need for methodological development on these issues specific to plants, which attract much less attention from methodologists than issues related to the monitoring of vertebrate populations. Furthermore, the sessile nature of plants offers op-

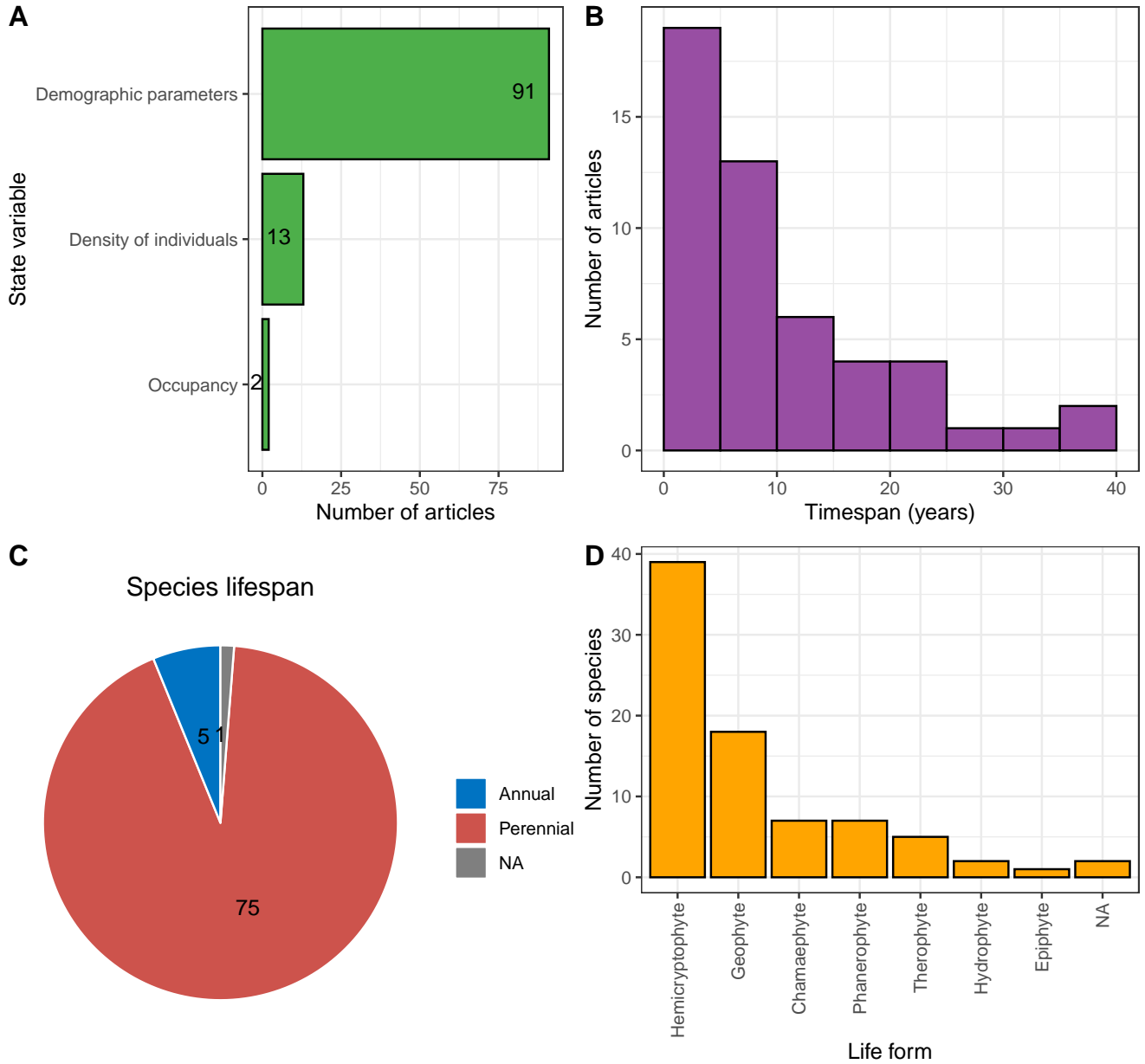


FIGURE 1.2 – Description of the analysed corpus of articles. The plots refer only to the relevant articles. (A) The number of articles in which each state variable is estimated (some articles estimate more than one state variable). (B) Timespan of the analysed population monitoring (this information was missing for 46 articles out of 96). (C) The lifespan of the studied species. (D) Raunkiaer life form of the studied species.

opportunities for methodological developments that could make monitoring programmes more efficient.

The density of individuals is the only state variable that can be estimated by both population-level (N-mixture) and individual monitoring (closed population CR). For plants, marking individuals can be difficult, if not impossible, for small species occurring at high densities. Thus, the N-mixture method should be preferred for such species. Otherwise, the difference in estimate precision between the N-mixture and the closed population CR methods mainly depends on the time needed to mark the individuals since, with the N-mixture method, this time can instead be devoted to prospecting more spatial units or making more visits. However, the N-mixture method is less robust to violation of the underlying assumptions than closed population CR, and uncontrolled variation of detection probability between detection occasions or individuals can lead to unidentifiable parameters (BARKER et al., 2018). In such situations, the CR method should be preferred to the N-mixture method.

Population-level monitoring is little used in research (Box 2) since it does not allow an understanding of the mechanisms driving population dynamics, which is nowadays the main focus of most research in plant population dynamics. However, conservationists extensively use population-level monitoring, but most of these studies are to be searched in the grey literature if ever published (CORLETT, 2011). Thus, it is crucial to ensure that there is no lack of methodological development on population-level monitoring methods because researchers seldom use them. Moreover, individual monitoring is mainly carried out on species types that raise the least methodological issues, i.e. conspicuous perennial species with differentiable individuals (Box 2). For these species types, it is possible to estimate demographic parameters using standard methods developed to study vertebrates. Thus, there could be a lack of methodological development to adapt individual monitoring methods to species types that raise methodological issues specific to plants, such as annual species and species for which individuals are difficult or impossible to delimit.

1.4.2 Improving sampling designs

In plant populations, individuals are often aggregated at multiple spatial scales. For instance, plant species are often restricted to a given habitat, patches of which are aggregated in the landscape. Within occupied patches, individuals may be aggregated due to limited seed dispersal (LARA-ROMERO et al., 2016; LEVIN, 1992). Spatially nested sampling designs (e.g. LARK & CORSTANJE, 2009; WEBSTER et al., 2006) could be efficient to monitor this type of species but have seldom been used. Little is known about their performance compared to conventional designs. Adaptive sampling methods such as ACS could also be used at some spatial scales of multi-scale sampling designs to increase the precision of temporal trend estimates, but this has never been done. Similarly, the performance of adaptive sampling methods to estimate temporal trends relative to fixed quadrats drawn with one-step sampling methods is unknown, as most adaptive sampling studies focus on point estimates. Globally, many studies on improving sampling methods focus on point estimates, and the literature is sparse concerning their extension to the temporal dimension. Another issue that has not yet been addressed in the sampling literature and is likely to become more and more frequent with climate change is the spatial shift of populations. For instance, mountain plant species may colonise sites at higher elevations and disappear from sites at lower elevations (LENOIR et al., 2008). Thus, a monitoring programme based on a statistical population defined by elevation limits will observe a population decline simply because the definition of the statistical population is no longer appropriate. Addressing this requires adapting the statistical population over time, for example, by estimating the colonisation speed of the species at its upper margin and dynamically adding new sampling units in the colonised areas.

1.4.3 Using drones

Drones equipped with cameras are growingly used in ecology because they allow data collection over large areas faster than ground surveys (CORCORAN et al., 2021). For the study of plants, drones were first used to monitor the exploitation of tropical forests (KOH & WICH, 2012) and to detect invasive tree or shrub species at the landscape scale (LEHMANN et al., 2017). Subsequently, an interest has developed in using

drones to study plant population dynamics at smaller spatial scales (TAY et al., 2018). Notably, ROMINGER et al. (2021) performed the first individual monitoring study using drones on the dwarf bear poppy (*Arctomecon humilis*), an endangered desert species. Using drone images from two subsequent years, human observers georeferenced all the individuals in the images, and recruitment, mortality and plant growth were estimated from these individual monitoring data.

Drones make it possible to generate large amounts of images, which can be very labour-intensive to analyse if done by human observers. Thus, using machine learning algorithms to process images automatically is a promising perspective that could unlock drones' full potential to study population dynamics. Tools to automatically detect invasive plants have already been developed (JAMES & BRADSHAW, 2020; TAY et al., 2018), but to date, there has been no application for other population monitoring studies. For drones to be usable for this purpose, it will be necessary to carry out methodological studies to understand up to what level of inconspicuousness of the studied species drone images can be used. Furthermore, the observation process will have to be modelled as for traditional ground surveys carried out by human observers (DAMGAARD, 2021).

1.4.4 Integrate the seed bank in population-level monitoring

Seed banks form an important part of the life cycle of many plant species and play an essential role in maintaining population viability, genetic diversity, and adaptive capacities (Harper 1977, Thompson et al. 1997). For many pioneer species, going through local extinctions and spectacular re-emergences following disturbances is common (GAZAIX et al., 2020). Without information on the number of seeds in the seed bank and their potential duration of dormancy, it is impossible to know whether a population decline or extinction should be of concern or part of a natural cycle (FRECKLETON & WATKINSON, 2003). Estimating state variables of the seed bank, such as the number of seeds in the seed bank, annual germination probability and maximum dormancy duration, is possible in individual monitoring studies, including measures of seed production per plant and germination experiments on seeds collected in the field (see for example ANDRIEU et al., 2017). However, estimating these parameters in population-level monitoring studies is challenging. Historically, the only way relied on direct measurements of the number of seeds in the soil by collecting soil samples, sifting them, counting

the gathered seeds and performing germination experiments in the lab (THOMPSON & GRIME, 1979). This approach provides valuable information on the seed bank but is very labour-intensive and partly destructive as it requires soil removal. In addition, seed germination is triggered by environmental conditions such as humidity, temperature and the photoperiod (HARPER, 1977). Thus, germination rates estimated *ex situ* are likely to be different from those under natural conditions and may fail to predict the role of the seed bank in population dynamics (PLUNTZ et al., 2018). To solve these issues, methods have been developed over the last ten years to infer seed bank state variables without direct observation using Hidden Markov Models (HMM). In these models, the seed bank parameters are modelled as latent variables indirectly observed through population-level measures such as occupancy (FRÉVILLE et al., 2013) or abundance classes (LE COZ et al., 2019). Initially, these methods were restricted to the study of metapopulations, in which a species could colonise an unoccupied site from adjacent sites or the seed bank. However, generalisations have been implemented for populations without a metapopulation structure (PLUNTZ et al., 2018). These methods do not require additional fieldwork compared to a classical population monitoring protocol and allow estimating the seed bank parameters under real conditions, which avoids the sometimes risky extrapolation of laboratory results. These methods are very recent, and most studies are based on simulations (but see PLUNTZ et al., 2018). Studies are needed to test their implementation under real conditions, but they are a promising perspective for better understanding the role of seed banks in plant population dynamics.

1.4.5 Integrated population models

The state variables characterising the individuals (e.g. survival and fecundity) and the population (e.g. density of individuals) are linked by demographic processes, i.e. individual survival and fecundity determine the future density of individuals of the population. However, most monitoring studies estimate individual and population-level state variables separately. This dichotomy has been resolved by developing integrated population models (hereafter, 'IPM', BESBEAS et al., 2002). IPMs combine multiple data types (usually count data and individual monitoring data) into a single statistical model, linking, for example, changes in the density of individuals and demographic parameters via a population matrix model. The advantages of this approach compared to analysing

each data type separately are that more state variables can be estimated as there is information about multiple demographic processes, that estimations are more precise as the data sets share information, and that all sources of uncertainty are included in the measure of parameter uncertainty (SCHAUB & ABADI, 2011). IPMs are particularly suited to studying rare and threatened species for which data is often sparse, as they allow to use all available information sources (ZIPKIN & SAUNDERS, 2018). IPMs have been an extremely dynamic subject of methodological research since their first development. Their early forms allowed the study of the simplest demographic processes, such as survival, recruitment and population size trends. However, IPMs are now a flexible framework allowing to study processes as diverse as source-sink dynamics, synchrony within metapopulations, density-dependent effects on demographic parameters (ZIPKIN & SAUNDERS, 2018), and even jointly estimating the effects of climate and interspecific relationships on populations (QUÉROUÉ et al., 2021). IPMs were initially developed to study bird and mammal populations, and to date, no study using IPMs on plants has been published.

1.4.6 Dichotomy between existing tools and practices

Many methodological developments have been made since the last guide on plant population monitoring was published (ELZINGA & SALZER, 1998). In 1998, the only existing methods to correct for observation errors were distance sampling and capture-recapture methods, which had never been used for plants (Box 1). Since then, methods have been developed to model the observation process at the population and individual levels, whatever the state variable of interest. All the methods presented in this review have been applied to plant populations except for the N-mixture method. Despite these methodological advances and the numerous perspectives for future developments, the estimation of the detection probability remains exceptional for plants (Box 2; KELLNER & SWIHART, 2014), and judgement sampling still seems to be common. Several reasons could explain this dichotomy between the existing tools and the practices of plant ecologists. The methods to correct for observation errors were primarily developed for vertebrates, and there may be transferability issues for some plant species (e.g. difficult to differentiate individuals and high densities of individuals). There is also a lack of awareness of plant ecologists to the problem of imperfect detection, a lack of interest

in plant-specific methods, and, consequently, a lack of interaction between methodologists and plant ecologists. However, we believe that there is a growing awareness of detection issues among plant ecologists, as suggested by the rapid adoption of the DND site occupancy method and the development of TTD for plants (Box 1).

1.4.7 Leverages to help improve the design of plant population monitoring studies

Practices regarding observation errors in plant studies are changing, as illustrated by the adoption of the methods described in Box 1 and the rapid use of the time-to-detection method. One of our aims with this review is to encourage this change. One of the ways to encourage the adoption of these methods is to alleviate the constraint of doing repeated visits on all sampling units, which is a heavy logistical constraint in many field surveys. Methodological studies have to be conducted to provide guidelines on the design of plant population monitoring studies where repeated visits are made on a subset of sampling units. Another avenue is data integration and integrated population models, especially methods integrating opportunistic observations. These methods could increase the precision of estimates without increasing study costs and help to better understand plant population dynamics by making it possible to answer questions that were impossible to study because of a lack of powerful enough methods. Exploring these avenues and improving the design of plant population monitoring studies will require more collaboration between plant ecologists and methodologists. Therefore, we call for more dialogue between these two communities to initiate collaborative research programmes and create joint research units between conservationists, plant ecologists and methodologists.

References

- ALEXANDER, H. M., SLADE, N. A., & KETTLE, W. D. (1997). Application of mark-recapture models to estimation of the population size of plants. *Ecology*, 78(4), 1230-1237. [https://doi.org/10.1890/0012-9658\(1997\)078\[1230:AOMRMT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1230:AOMRMT]2.0.CO;2) (cf. p. 41, 59, 62, 64, 65)
- ANDERSON, D. R. (2001). The Need to Get the Basics Right in Wildlife Field Studies. *Wildlife Society Bulletin (1973-2006)*, 29(4), 1294-1297 (cf. p. 40).

- ANDRELLO, M., NICOLE, F., TILL-BOTTRAUD, I., & GAGGIOTTI, O. E. (2012). Effect of Stage-Specific Vital Rates on Population Growth Rates and Effective Population Sizes in an Endangered Iteroparous Plant. *Conservation Biology*, 26(2), 208-217. <https://doi.org/10.1111/j.1523-1739.2011.01815.x> (cf. p. 63)
- ANDRIEU, E., BESNARD, A., FRÉVILLE, H., VAUDEY, V., GAUTHIER, P., THOMPSON, J. D., & DEBUSSCHE, M. (2017). Population dynamics of *Paeonia officinalis* in relation to forest closure : From model predictions to practical conservation management. *Biological Conservation*, 215, 51-60. <https://doi.org/10.1016/j.biocon.2017.08.010> (cf. p. 59, 65, 66, 74)
- ARCHAUX, F., HENRY, P.-Y., & GIMENEZ, O. (2012). When can we ignore the problem of imperfect detection in comparative studies? *Methods in Ecology and Evolution*, 3(1), 188-194. <https://doi.org/10.1111/j.2041-210X.2011.00142.x> (cf. p. 40, 41)
- BARKER, R. J., SCHOFIELD, M. R., LINK, W. A., & SAUER, J. R. (2018). On the reliability of N-mixture models for count data. *Biometrics*, 74(1), 369-377. <https://doi.org/10.1111/biom.12734> (cf. p. 72)
- BERBERICH, G. M., DORMANN, C. F., KLIMETZEK, D., BERBERICH, M. B., SANDERS, N. J., & ELLISON, A. M. (2016). Detection probabilities for sessile organisms. *Ecosphere*, 7(11), e01546. <https://doi.org/10.1002/ecs2.1546> (cf. p. 41)
- BESBEAS, P., FREEMAN, S. N., MORGAN, B. J. T., & CATCHPOLE, E. A. (2002). Integrating Mark-Recapture-Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters. *Biometrics*, 58(3), 540-547 (cf. p. 75).
- BJØRNSTAD, O. N., & GRENFELL, B. T. (2001). Noisy clockwork : time series analysis of population fluctuations in animals. *Science*, 293(5530), 638-643. <https://doi.org/10.1126/science.1062226> (cf. p. 39)
- BOLKER, B. M. (2008). 6. Likelihood and All That. In *Ecological Models and Data in R* (p. 169-221). Princeton University Press. <https://doi.org/10.1515/9781400840908-007>. (Cf. p. 54)
- BORNAND, C. N., KERY, M., BUECHE, L., & FISCHER, M. (2014). Hide-and-seek in vegetation : time-to-detection is an efficient design for estimating detectability and occurrence. *Methods in Ecology and Evolution*, 5(5), 433-442. <https://doi.org/10.1111/2041-210X.12171> (cf. p. 53, 55)
- BRAUN-BLANQUET, J. (1964). *Pflanzensoziologie : Grundzüge der Vegetationskunde*. Springer. (Cf. p. 57).
- BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P., & LAAKE, J. L. (1993). *Distance Sampling : Estimating Abundance of Biological Populations*. Chapman & Hall. (Cf. p. 56).
- CALENGE, C., MÉNONI, E., MILHAU, B., FOULCHÉ, K., CHIFFARD, J., & MARCHANDEAU, S. (2022). Estimating the population size of a mountain galliform in the context of multi-stakeholder adaptive management. *Ecological Applications*, n/a(n/a), e2746. <https://doi.org/10.1002/eap.2746> (cf. p. 44)
- CARIGNAN, V., & VILLARD, M.-A. (2002). Selecting Indicator Species to Monitor Ecological Integrity : A Review. *Environmental Monitoring and Assessment*, 78(1), 45-61. <https://doi.org/10.1023/A:1016136723584> (cf. p. 60)
- CASWELL, H. (2001). *Matrix Population Models : Construction, Analysis, and Interpretation*. Sinauer Associates. (Cf. p. 67, 68).
- CHANDLER, R., KELLNER, K., FISKE, I., MILLER, D., ROYLE, A., HOSTETLER, J., HUTCHINSON, R., SMITH, A., KERY, M., MEREDITH, M., FOURNIER, A.,

- MULDOON, A., & BAKER, C. (2022). unmarked : Models for Data from Unmarked Animals. (Cf. p. 54).
- CHARPENTIER, A., KREDER, M., BESNARD, A., GAUTHIER, P., & BOUFFET, C. (2020). How *Cortaderia selloana*, an ornamental plant considered highly invasive, fails to spread from urban to natural habitats in Southern France. *Urban Ecosystems*, 23(6), 1181-1190. <https://doi.org/10.1007/s11252-020-01003-4> (cf. p. 56)
- CHEN, G., KÉRY, M., PLATTNER, M., MA, K., & GARDNER, B. (2013). Imperfect detection is the rule rather than the exception in plant distribution studies. *Journal of Ecology*, 101(1), 183-191. <https://doi.org/10.1111/1365-2745.12021> (cf. p. 41, 53)
- CHEN, G., KÉRY, M., ZHANG, J., & MA, K. (2009). Factors affecting detection probability in plant distribution studies. *Journal of Ecology*, 97(6), 1383-1389. <https://doi.org/10.1111/j.1365-2745.2009.01560.x> (cf. p. 41, 53)
- CHIFFARD, J., MARCIAU, C., YOCCOZ, N. G., MOUILLOT, F., DUCHATEAU, S., NADEAU, I., FONTANILLES, P., & BESNARD, A. (2020). Adaptive niche-based sampling to improve ability to find rare and elusive species : Simulations and field tests. *Methods in Ecology and Evolution*, n/a(n/a). <https://doi.org/10.1111/2041-210X.13399> (cf. p. 47)
- COCHRAN, W. G. (1977). *Sampling Techniques* (3rd). John Wiley & Sons. (Cf. p. 40, 43, 45, 47).
- CORCORAN, E., WINSEN, M., SUDHOLZ, A., & HAMILTON, G. (2021). Automated detection of wildlife using drones : Synthesis, opportunities and constraints. *Methods in Ecology and Evolution*, 12(6), 1103-1114. <https://doi.org/10.1111/2041-210X.13581> (cf. p. 73)
- CORLETT, R. T. (2011). Trouble with the Gray Literature. *Biotropica*, 43(1), 3-5. <https://doi.org/10.1111/j.1744-7429.2010.00714.x> (cf. p. 72)
- CORMACK, R. M. (1964). Estimates of Survival from the Sighting of Marked Animals. *Biometrika*, 51(3/4), 429-438. <https://doi.org/10.2307/2334149> (cf. p. 41)
- COUTURIER, T., CHEYLAN, M., BERTOLERO, A., ASTRUC, G., & BESNARD, A. (2013). Estimating abundance and population trends when detection is low and highly variable : A comparison of three methods for the Hermann's tortoise. *The Journal of Wildlife Management*, 77(3), 454-462. <https://doi.org/10.1002/jwmg.499> (cf. p. 41)
- DAMGAARD, C. (2021). Integrating Hierarchical Statistical Models and Machine-Learning Algorithms for Ground-Truthing Drone Images of the Vegetation : Taxonomy, Abundance and Population Ecological Models. *Remote Sensing*, 13(6), 1161. <https://doi.org/10.3390/rs13061161> (cf. p. 74)
- DAMGAARD, C. F., & IRVINE, K. M. (2019). Using the beta distribution to analyse plant cover data. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13200> (cf. p. 45, 57)
- DELANEY, D. G., & LEUNG, B. (2010). An empirical probability model of detecting species at low densities. *Ecological Applications*, 20(4), 1162-1172. <https://doi.org/10.1890/09-0309.1> (cf. p. 41)
- DENNIS, B., MUNHOLLAND, P. L., & SCOTT, J. M. (1991). Estimation of Growth and Extinction Parameters for Endangered Species. *Ecological Monographs*, 61(2), 115-143. <https://doi.org/10.2307/1943004> (cf. p. 39)
- DUCHENNE, F., PORCHER, E., MIHOUB, J.-B., LOÏS, G., & FONTAINE, C. (2022). Controversy over the decline of arthropods : a matter of temporal baseline?

- Peer Community Journal*, 2. <https://doi.org/10.24072/pcjournal.131> (cf. p. 43)
- EASTERLING, M. R., ELLNER, S. P., & DIXON, P. M. (2000). Size-Specific Sensitivity : Applying a New Structured Population Model. *Ecology*, 81(3), 694-708. [https://doi.org/10.1890/0012-9658\(2000\)081\[0694:SSSAAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2) (cf. p. 67)
- ELLNER, S. P., & REES, M. (2006). Integral Projection Models for Species with Complex Demography. *The American Naturalist*, 167(3), 410-428. <https://doi.org/10.1086/499438> (cf. p. 68)
- ELZINGA, C. L., & SALZER, D. W. (1998). *Measuring & Monitoring Plant Populations*. U.S. Department of the Interior, Bureau of Land Management. (Cf. p. 41, 76).
- FLETCHER, D., LEBRETON, J.-D., MARESCOT, L., SCHAUB, M., GIMENEZ, O., DAWSON, S., & SLOOTEN, E. (2012). Bias in estimation of adult survival and asymptotic population growth rate caused by undetected capture heterogeneity. *Methods in Ecology and Evolution*, 3(1), 206-216. <https://doi.org/10.1111/j.2041-210X.2011.00137.x> (cf. p. 63)
- FOURNIER, A. M., WHITE, E. R., & HEARD, S. B. (2019). Site-selection bias and apparent population declines in long-term studies. *Conservation Biology*, 33(6), 1370-1379. <https://doi.org/10.1111/cobi.13371> (cf. p. 44)
- FRECKLETON, R. P., & WATKINSON, A. R. (2003). Are all plant populations metapopulations? *Journal of Ecology*, 91(2), 321-324. <https://doi.org/10.1046/j.1365-2745.2003.00769.x> (cf. p. 74)
- FRÉVILLE, H., CHOQUET, R., PRADEL, R., & CHEPTOU, P.-O. (2013). Inferring seed bank from hidden Markov models : new insights into metapopulation dynamics in plants. *Journal of Ecology*, 101(6), 1572-1580. <https://doi.org/10.1111/1365-2745.12141> (cf. p. 75)
- GARRARD, G. E., BEKESY, S. A., MCCARTHY, M. A., & WINTLE, B. A. (2008). When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology*, 33(8), 986-998. <https://doi.org/10.1111/j.1442-9993.2008.01869.x> (cf. p. 41, 53-55)
- GARRARD, G. E., MCCARTHY, M. A., WILLIAMS, N. S. G., BEKESY, S. A., & WINTLE, B. A. (2013). A general model of detectability using species traits. *Methods in Ecology and Evolution*, 4(1), 45-52. <https://doi.org/10.1111/j.2041-210x.2012.00257.x> (cf. p. 53)
- GAZAIX, A., KLESCZEWSKI, M., BOUCHET, M.-A., CARTEREAU, M., MOLINA, J., MICHAUD, H., MULLER, S. D., PIRSOUL, L., GAUTHIER, P., GRILLAS, P., & THOMPSON, J. D. (2020). A history of discoveries and disappearances of the rare annual plant *Lythrum thesioides* M.Bieb. : new insights into its ecology and biology. *Botany Letters*, 167(2), 201-211. <https://doi.org/10.1080/23818107.2019.1684358> (cf. p. 41, 74)
- GERRODETTE, T. (1987). A Power Analysis for Detecting Trends. *Ecology*, 68(5), 1364-1372. <https://doi.org/10.2307/1939220> (cf. p. 43, 49)
- GILJOHANN, K. M., MCCARTHY, M. A., KEITH, D. A., KELLY, L. T., TOZER, M. G., & REGAN, T. J. (2017). Interactions between rainfall, fire and herbivory drive resprouter vital rates in a semi-arid ecosystem. *Journal of Ecology*, 105(6), 1562-1570. <https://doi.org/10.1111/1365-2745.12768> (cf. p. 59)
- GREIG-SMITH, P. (1983). *Quantitative Plant Ecology*. University of California Press. (Cf. p. 45).
- GUISAN, A., BROENNIMANN, O., ENGLER, R., VUST, M., YOCCOZ, N. G., LEHMANN, A., & ZIMMERMANN, N. E. (2006). Using Niche-Based Models

- to Improve the Sampling of Rare Species. *Conservation Biology*, 20(2), 501-511. <https://doi.org/10.1111/j.1523-1739.2006.00354.x> (cf. p. 41, 47)
- GUNTON, R. M., & KUNIN, W. E. (2009). Density-dependence at multiple scales in experimental and natural plant populations. *Journal of Ecology*, 97(3), 567-580. <https://doi.org/10.1111/j.1365-2745.2009.01492.x> (cf. p. 49)
- HAHN, I., & SCHEURING, I. (2003). The effect of measurement scales on estimating vegetation cover : a computer-assisted experiment. *Community Ecology*, 4(1), 29-33. <https://doi.org/10.1556/ComEc.4.2003.1.3> (cf. p. 57)
- HARPER, J. L., & WHITE, J. (1974). The Demography of Plants. *Annual Review of Ecology and Systematics*, 5, 419-463 (cf. p. 60).
- HARPER, J. L. (1977). *Population Biology of Plants*. Academic Press. (Cf. p. 75).
- HAUSER, C. E., GILJOHANN, K. M., MCCARTHY, M. A., GARRARD, G. E., ROBINSON, A. P., WILLIAMS, N. S. G., & MOORE, J. L. (2022). A field experiment characterizing variable detection rates during plant surveys. *Conservation Biology*, 36(3), e13888. <https://doi.org/10.1111/cobi.13888> (cf. p. 53)
- HENRY, D. A. W., LEE, A. T. K., & ALTWEGG, R. (2020). Can time-to-detection models with fewer survey replicates provide a robust alternative to traditional site-occupancy models? *Methods in Ecology and Evolution*, 11(5), 643-655. <https://doi.org/10.1111/2041-210X.13379> (cf. p. 55)
- IRVINE, K. M., WRIGHT, W. J., SHANAHAN, E. K., & RODHOUSE, T. J. (2019). Cohesive framework for modelling plant cover class data. *Methods in Ecology and Evolution*, 10(10), 1749-1760. <https://doi.org/https://doi.org/10.1111/2041-210X.13262> (cf. p. 58)
- ISAAC, N. J. B., JARZYNA, M. A., KEIL, P., DAMBLY, L. I., BOERSCH-SUPAN, P. H., BROWNING, E., FREEMAN, S. N., GOLDING, N., GUILLERA-ARROITA, G., HENRYS, P. A., JARVIS, S., LAHOZ-MONFORT, J., PAGEL, J., PEScott, O. L., SCHMUCKI, R., SIMMONDS, E. G., & O'HARA, R. B. (2020). Data Integration for Large-Scale Models of Species Distributions. *Trends in Ecology & Evolution*, 35(1), 56-67. <https://doi.org/10.1016/j.tree.2019.08.006> (cf. p. 59)
- IUCN. (2019). Guidelines for Using the IUCN Red List Categories and Criteria - Version 14. (Cf. p. 39).
- JAMES, K., & BRADSHAW, K. (2020). Detecting plant species in the field with deep learning and drone technology. *Methods in Ecology and Evolution*, 11(11), 1509-1519. <https://doi.org/https://doi.org/10.1111/2041-210X.13473> (cf. p. 74)
- JIMÉNEZ-ALFARO, B., & IRIONDO, J. (2014). Population dynamics of *Aster pyrenaicus* Desf., a threatened species of temperate forest edges : A view of meso- and micro-scales. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 148(4), 645-654. <https://doi.org/10.1080/11263504.2013.788094> (cf. p. 65)
- JOLLY, G. M. (1965). Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. *Biometrika*, 52(1/2), 225-247. <https://doi.org/10.2307/2333826> (cf. p. 41)
- KALTON, G., & ANDERSON, D. W. (1986). Sampling Rare Populations. *Journal of the Royal Statistical Society. Series A (General)*, 149(1), 65-82. <https://doi.org/10.2307/2981886> (cf. p. 46)
- KATTGE, J., BÖNISCH, G., DÍAZ, S., LAVOREL, S., PRENTICE, I. C., LEADLEY, P., TAUTENHAHN, S., WERNER, G. D. A., AAKALA, T., ABEDI, M., ACOSTA, A. T. R., ADAMIDIS, G. C., ADAMSON, K., AIBA, M., ALBERT, C. H.,

- ALCÁNTARA, J. M., ALCÁZAR C, C., ALEIXO, I., ALI, H., ... WIRTH, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26(1), 119-188. <https://doi.org/10.1111/gcb.14904> (cf. p. 69)
- KELLNER, K. F., & SWIHART, R. K. (2014). Accounting for Imperfect Detection in Ecology : A Quantitative Review. *Plos One*, 9(10), e111436. <https://doi.org/10.1371/journal.pone.0111436> (cf. p. 41, 60, 76)
- KERMORVANT, C., COUBE, S., D'AMICO, F., BRU, N., & CAILL-MILLY, N. (2020). Sequential process to choose efficient sampling design based on partial prior information data and simulations. *Spatial Statistics*, 38, 100439. <https://doi.org/10.1016/j.spasta.2020.100439> (cf. p. 46)
- KERMORVANT, C., D'AMICO, F., BRU, N., CAILL-MILLY, N., & ROBERTSON, B. (2019). Spatially balanced sampling designs for environmental surveys. *Environmental Monitoring and Assessment*, 191(8), 524. <https://doi.org/10.1007/s10661-019-7666-y> (cf. p. 45)
- KÉRY, M., GREGG, K. B., & SCHAUB, M. (2005). Demographic estimation methods for plants with unobservable life-states. *Oikos*, 108(2), 307-320. <https://doi.org/10.1111/j.0030-1299.2005.13589.x> (cf. p. 59, 66)
- KÉRY, M., DORAZIO, R. M., SOLDAAT, L., van STRIEN, A., ZUIDERWIJK, A., & ROYLE, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, 46(6), 1163-1172. <https://doi.org/10.1111/j.1365-2664.2009.01724.x> (cf. p. 41, 56)
- KÉRY, M., & GREGG, K. B. (2003). Effects of life-state on detectability in a demographic study of the terrestrial orchid *Cleistes bifaria*. *Journal of Ecology*, 91(2), 265-273. <https://doi.org/10.1046/j.1365-2745.2003.00759.x> (cf. p. 59, 62, 64-66)
- KÉRY, M., ROYLE, J. A., HALLMAN, T., ROBINSON, W. D., STREBEL, N., & KELLNER, K. F. (2022). Integrated distance sampling models for simple point counts. <https://doi.org/10.48550/arXiv.2211.17229>. (Cf. p. 59)
- KOH, L. P., & WICH, S. A. (2012). Dawn of Drone Ecology : Low-Cost Autonomous Aerial Vehicles for Conservation. *Tropical Conservation Science*, 5(2), 121-132. <https://doi.org/10.1177/194008291200500202> (cf. p. 73)
- KOSHKINA, V., WANG, Y., GORDON, A., DORAZIO, R. M., WHITE, M., & STONE, L. (2017). Integrated species distribution models : combining presence-background data and site-occupancy data with imperfect detection. *Methods in Ecology and Evolution*, 8(4), 420-430. <https://doi.org/10.1111/2041-210X.12738> (cf. p. 59)
- LARA-ROMERO, C., CRUZ, M. d. I., ESCRIBANO-ÁVILA, G., GARCÍA-FERNÁNDEZ, A., & IRIONDO, J. M. (2016). What causes conspecific plant aggregation ? Disentangling the role of dispersal, habitat heterogeneity and plant–plant interactions. *Oikos*, 125(9), 1304-1313. <https://doi.org/https://doi.org/10.1111/oik.03099> (cf. p. 45, 49, 73)
- LARK, R. M., & CORSTANJE, R. (2009). Non-homogeneity of variance components from spatially nested sampling of the soil. *European Journal of Soil Science*, 60(3), 443-452. <https://doi.org/10.1111/j.1365-2389.2009.01133.x> (cf. p. 73)
- LAROCHE, F. (2022). Efficient sampling designs to assess biodiversity spatial autocorrelation : should we go fractal ? <https://doi.org/10.1101/2022.07.29.501974>. (Cf. p. 45)
- LAVERGNE, S., THOMPSON, J. D., GARNIER, E., & DEBUSSCHE, M. (2004). The biology and ecology of narrow endemic and widespread plants : a comparative

- study of trait variation in 20 congeneric pairs. *Oikos*, 107(3), 505-518. <https://doi.org/10.1111/j.0030-1299.2004.13423.x> (cf. p. 41)
- LE COZ, S., CHEPTOU, P.-O., & PEYRARD, N. (2019). A spatial Markovian framework for estimating regional and local dynamics of annual plants with dormancy. *Theoretical Population Biology*, 127, 120-132. <https://doi.org/10.1016/j.tpb.2019.03.002> (cf. p. 75)
- LEBRETON, J.-D., BURNHAM, K. P., CLOBERT, J., & ANDERSON, D. R. (1992). Modeling Survival and Testing Biological Hypotheses Using Marked Animals : A Unified Approach with Case Studies. *Ecological Monographs*, 62(1), 67-118. <https://doi.org/10.2307/2937171> (cf. p. 40, 66)
- LEGENDRE, P. (1993). Spatial Autocorrelation : Trouble or New Paradigm? *Ecology*, 74(6), 1659-1673. <https://doi.org/10.2307/1939924> (cf. p. 45)
- LEGG, C. J., & NAGY, L. (2006). Why most conservation monitoring is, but need not be, a waste of time. *Journal of Environmental Management*, 78(2), 194-199. <https://doi.org/10.1016/j.jenvman.2005.04.016> (cf. p. 39, 40, 49)
- LEHMANN, J. R. K., PRINZ, T., ZILLER, S. R., THIELE, J., HERINGER, G., MEIRANETO, J. A. A., & BUTTSCHARDT, T. K. (2017). Open-Source Processing and Analysis of Aerial Imagery Acquired with a Low-Cost Unmanned Aerial System to Support Invasive Plant Management. *Frontiers in Environmental Science*, 5 (cf. p. 73).
- LENOIR, J., GEGOUT, J. C., MARQUET, P. A., de RUFFRAY, P., & BRISSE, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768-1771. <https://doi.org/10.1126/science.1156831> (cf. p. 73)
- LEVIN, S. A. (1992). The Problem of Pattern and Scale in Ecology. *Ecology*, 73(6), 1943-1967. <https://doi.org/10.2307/1941447> (cf. p. 45, 73)
- LINCOLN, F. C. (1930). *Calculating waterfowl abundance on the basis of banding returns*. Washington, D.C. : U.S. Dept. of Agriculture. (Cf. p. 41).
- LINDENMAYER, D. B., GIBBONS, P., BOURKE, M., BURGMAN, M., DICKMAN, C. R., FERRIER, S., FITZSIMONS, J., FREUDENBERGER, D., GARNETT, S. T., GROVES, C., HOBBS, R. J., KINGSFORD, R. T., KREBS, C., LEGGE, S., LOWE, A. J., MCLEAN, R., MONTAMBAULT, J., POSSINGHAM, H., RADFORD, J., ... ZERGER, A. (2012). Improving biodiversity monitoring. *Austral Ecology*, 37(3), 285-294. <https://doi.org/10.1111/j.1442-9993.2011.02314.x> (cf. p. 39, 40)
- LINDENMAYER, D. B., & LIKENS, G. E. (2009). Adaptive monitoring : a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution*, 24(9), 482-486. <https://doi.org/10.1016/j.tree.2009.03.005> (cf. p. 40)
- LOUVRIER, J., DUCHAMP, C., LAURET, V., MARBOUTIN, E., CUBAYNES, S., CHOQUET, R., MIQUEL, C., & GIMENEZ, O. (2018). Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. *Ecography*, 41(4), 647-660. <https://doi.org/10.1111/ecog.02874> (cf. p. 52)
- LOVETT, G. M., BURNS, D. A., DRISCOLL, C. T., JENKINS, J. C., MITCHELL, M. J., RUSTAD, L., SHANLEY, J. B., LIKENS, G. E., & HAEUBER, R. (2007). Who needs environmental monitoring? *Frontiers in Ecology and the Environment*, 5(5), 253-260. [https://doi.org/10.1890/1540-9295\(2007\)5\[253:WNEM\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[253:WNEM]2.0.CO;2) (cf. p. 39)
- MACKENZIE, D. I., NICHOLS, J. D., HINES, J. E., KNUTSON, M. G., & FRANKLIN, A. B. (2003). Estimating site occupancy, colonization, and local extinction when

- a species is detected imperfectly. *Ecology*, 84(8), 2200-2207. <https://doi.org/10.1890/02-3090> (cf. p. 52, 55)
- MACKENZIE, D. I., NICHOLS, J. D., LACHMAN, G. B., DROEGE, S., ROYLE, J. A., & LANGTIMM, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248-2255. <https://doi.org/10.2307/3072056> (cf. p. 41, 53)
- MACKENZIE, D. I., NICHOLS, J. D., ROYLE, J. A., POLLOCK, K. H., BAILEY, L. L., & HINES, J. E. (2017, novembre 17). *Occupancy estimation and modeling : inferring patterns and dynamics of species occurrence*. Elsevier. (Cf. p. 54).
- MACKENZIE, D. I., & ROYLE, J. A. (2005). Designing occupancy studies : general advice and allocating survey effort. *Journal of Applied Ecology*, 42(6), 1105-1114. <https://doi.org/10.1111/j.1365-2664.2005.01098.x> (cf. p. 54)
- MCGARVEY, R., BURCH, P., & MATTHEWS, J. M. (2016). Precision of systematic and random sampling in clustered populations : habitat patches and aggregating organisms. *Ecological Applications*, 26(1), 233-248. <https://doi.org/10.1890/14-1973> (cf. p. 45)
- MILBERG, P., BERGSTEDT, J., FRIDMAN, J., ODELL, G., & WESTERBERG, L. (2008). Observer bias and random variation in vegetation monitoring data. *Journal of Vegetation Science*, 19(5), 633-644. <https://doi.org/10.3170/2008-8-18423> (cf. p. 57)
- MOORE, J. L., HAUSER, C. E., BEAR, J. L., WILLIAMS, N. S. G., & MCCARTHY, M. A. (2011). Estimating detection-effort curves for plants using search experiments. *Ecological Applications*, 21(2), 601-607. <https://doi.org/10.1890/10-0590.1> (cf. p. 53)
- MORRISON, L. W., SMITH, D., YOUNG, C., & NICHOLS, D. (2008). Evaluating sampling designs by computer simulation : A case study with the Missouri bladderpod. *Population Ecology*, 50(4), 9. <https://doi.org/10.1007/s10144-008-0100-x> (cf. p. 46)
- MOZZHERIN, D., MYLTSEV, A., & ZALAVADIYA, H. (2022). gnames/gnfinder : v1.0.1. <https://doi.org/10.5281/zenodo.7131329>. (Cf. p. 69)
- NIC LUGHADHA, E., BACHMAN, S. P., LEÃO, T. C. C., FOREST, F., HALLEY, J. M., MOAT, J., ACEDO, C., BACON, K. L., BREWER, R. F. A., GÂTEBLÉ, G., GONÇALVES, S. C., GOVAERTS, R., HOLLINGSWORTH, P. M., KRISAI-GREILHUBER, I., de LIRIO, E. J., MOORE, P. G. P., NEGRÃO, R., ONANA, J. M., RAJAOVELONA, L. R., ... WALKER, B. E. (2020). Extinction risk and threats to plants and fungi. *PLANTS, PEOPLE, PLANET*, 2(5), 389-408. <https://doi.org/10.1002/ppp3.10146> (cf. p. 41)
- NICHOLS, J. D., & WILLIAMS, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution*, 21(12), 668-673. <https://doi.org/10.1016/j.tree.2006.08.007> (cf. p. 39, 44)
- OTIS, D. L., BURNHAM, K. P., WHITE, G. C., & ANDERSON, D. R. (1978). Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs*, (62), 3-135 (cf. p. 40, 64, 65).
- PALMER, M. W. (1993). Potential biases in site and species selection for ecological monitoring. *Environmental Monitoring and Assessment*, 26(2), 277-282. <https://doi.org/10.1007/BF00547504> (cf. p. 44)
- PECHMANN, J. H. K., SCOTT, D. E., SEMLITSCH, R. D., CALDWELL, J. P., VITT, L. J., & GIBBONS, J. W. (1991). Declining Amphibian Populations : The Problem of Separating Human Impacts from Natural Fluctuations. *Science*, 253(5022), 892-895. <https://doi.org/10.1126/science.253.5022.892> (cf. p. 44)

- PERRET, J., BESNARD, A., CHARPENTIER, A., & PAPUGA, G. (2023). Plants stand still but hide : imperfect and heterogeneous detection is the rule when counting plants. *Journal of Ecology*, 111. <https://doi.org/10.1111/1365-2745.14110> (cf. p. 41, 53)
- PERRET, J., CHARPENTIER, A., PRADEL, R., PAPUGA, G., & BESNARD, A. (2022). Spatially balanced sampling methods are always more precise than random ones for estimating the size of aggregated populations. *Methods in Ecology and Evolution*, 13(12), 2743-2756. <https://doi.org/10.1111/2041-210X.14015> (cf. p. 45, 46)
- PETERSEN, C. G. (1896). The yearly immigration of young plaice into the Limfjord from the German Sea. *Report of the Danish Biological Station*, 6, 1-48 (cf. p. 41).
- PETERSON, S. A., URQUHART, N. S., & WELCH, E. B. (1999). Sample Representativeness : A Must for Reliable Regional Lake Condition Estimates. *Environmental Science & Technology*, 33(10), 1559-1565. <https://doi.org/10.1021/es9807111> (cf. p. 40)
- PHILIPPI, T. (2005). Adaptive Cluster Sampling for Estimation of Abundances Within Local Populations of Low-Abundance Plants. *Ecology*, 86(5), 1091-1100. <https://doi.org/10.1890/04-0621> (cf. p. 46)
- PIERCE, S., SPADA, A., CAPORALI, E., PUGLISI, F., PANZERI, A., LUZZARO, A., CISLAGHI, S., MANTEGAZZA, L., CARDARELLI, E., LABRA, M., GALIMBERTI, A., & CERIANI, R. M. (2018). Identifying population thresholds for flowering plant reproductive success : the marsh gentian (*Gentiana pneumonanthe*) as a flagship species of humid meadows and heathland. *Biodiversity and Conservation*, 27(4), 891-905. <https://doi.org/10.1007/s10531-017-1470-1> (cf. p. 48)
- PLUNTZ, M., LE COZ, S., PEYRARD, N., PRADEL, R., CHOQUET, R., & CHEPTOU, P.-O. (2018). A general method for estimating seed dormancy and colonisation in annual plants from the observation of existing flora. *Ecology Letters*, 21(9), 1311-1318. <https://doi.org/10.1111/ele.13097> (cf. p. 75)
- QUÉROUÉ, M., BARBRAUD, C., BARRAQUAND, F., TUREK, D., DELORD, K., PACOUREAU, N., & GIMENEZ, O. (2021). Multispecies integrated population model reveals bottom-up dynamics in a seabird predator-prey system. *Ecological Monographs*, 91(3), e01459. <https://doi.org/10.1002/ecm.1459> (cf. p. 76)
- RABINOWITZ, D. (1981). Seven forms of rarity, 14 (cf. p. 46).
- RAUNKIÆR, C. (1934). *The Life Forms of Plants and Statistical Plant Geography Being the Collected Papers of C. Raunkiaer*. Oxford at the Clarendon Press. (Cf. p. 69).
- RHODES, J. R., & JONZEN, N. (2011). Monitoring temporal trends in spatially structured populations : how should sampling effort be allocated between space and time? *Ecography*, 34(6), 1040-1048. <https://doi.org/10.1111/j.1600-0587.2011.06370.x> (cf. p. 48)
- RIPPLE, W. J., & BESCHTA, R. L. (2012). Trophic cascades in Yellowstone : The first 15 years after wolf reintroduction. *Biological Conservation*, 145(1), 205-213. <https://doi.org/10.1016/j.biocon.2011.11.005> (cf. p. 39)
- RODHOUSE, T. J., IRVINE, K. M., & BOWERSOCK, L. (2020). Post-Fire Vegetation Response in a Repeatedly Burned Low-Elevation Sagebrush Steppe Protected Area Provides Insights About Resilience and Invasion Resistance. *Frontiers in Ecology and Evolution*, 8 (cf. p. 58).
- ROMINGER, K. R., DENITTIS, A., & MEYER, S. E. (2021). Using drone imagery analysis in rare plant demographic studies. *Journal for Nature Conservation*, 62, 126020. <https://doi.org/10.1016/j.jnc.2021.126020> (cf. p. 74)

- ROYLE, J. A., & LINK, W. A. (2006). Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, 87(4), 835-841. [https://doi.org/10.1890/0012-9658\(2006\)87\[835:GSOMAF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[835:GSOMAF]2.0.CO;2) (cf. p. 54)
- ROYLE, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, 60(1), 108-115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x> (cf. p. 41, 55)
- ROYLE, J. A., & NICHOLS, J. D. (2003). Estimating Abundance from Repeated Presence–Absence Data or Point Counts. *Ecology*, 84(3), 777-790. [https://doi.org/10.1890/0012-9658\(2003\)084\[0777:EAFRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2) (cf. p. 56)
- SAGARIN, R. D., & GAINES, S. D. (2002). Geographical abundance distributions of coastal invertebrates : using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography*, 29(8), 985-997. <https://doi.org/10.1046/j.1365-2699.2002.00705.x> (cf. p. 57)
- SCHAUB, M., & ABADI, F. (2011). Integrated population models : a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, 152(1), 227-237. <https://doi.org/10.1007/s10336-010-0632-7> (cf. p. 76)
- SEABLOOM, E. W., BJORNSTAD, O. N., BOLKER, B. M., & REICHMAN, O. J. (2005). Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecological Monographs*, 75(2), 199-214. <https://doi.org/10.1890/03-0841> (cf. p. 45)
- SEBER, G. A. F. (1965). A Note on the Multiple-Recapture Census. *Biometrika*, 52(1/2), 249-259. <https://doi.org/10.2307/2333827> (cf. p. 41)
- SHACKLETON, R. T., PETITPIERRE, B., PAJKOVIC, M., DESSIMOZ, F., BRÖNNIMANN, O., CATTIN, L., ČEJKOVÁ, Š., KULL, C. A., PERGL, J., PYŠEK, P., YOCCOZ, N., & GUISAN, A. (2020). Integrated Methods for Monitoring the Invasive Potential and Management of *Heracleum mantegazzianum* (giant hogweed) in Switzerland. *Environmental Management*, 65(6), 829-842. <https://doi.org/10.1007/s00267-020-01282-9> (cf. p. 46)
- SIMBERLOFF, D., MARTIN, J.-L., GENOVESI, P., MARIS, V., WARDLE, D. A., ARONSON, J., COURCHAMP, F., GALIL, B., GARCIA-BERTHOU, E., PASCAL, M., PYSEK, P., SOUSA, R., TABACCHI, E., & VILA, M. (2013). Impacts of biological invasions : what's what and the way forward. *Trends in Ecology & Evolution*, 28(1), 58-66. <https://doi.org/10.1016/j.tree.2012.07.013> (cf. p. 39)
- SKELLY, D. K., YUREWICZ, K. L., WERNER, E. E., & RELYEA, R. A. (2003). Estimating decline and distributional change in amphibians. *Conservation Biology*, 13(3), 744-751. <https://doi.org/http://doi.org/10.1046/j.1523-1739.2003.02009.x> (cf. p. 44)
- SMITH, A., ANDERSON, M. J., & PAWLEY, M. D. M. (2017). Could ecologists be more random? Straightforward alternatives to haphazard spatial sampling. *Ecography*, 40(11), 1251-1255. <https://doi.org/10.1111/ecog.02821> (cf. p. 40)
- STEVENS, D. L., & OLSEN, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association*, 99(465), 262-278. <https://doi.org/10.1198/016214504000000250> (cf. p. 41)
- STOUFFER, D. B. (2022). A critical examination of models of annual-plant population dynamics and density-dependent fecundity. *Methods in Ecology and Evolution*, 13(11), 2516-2530. <https://doi.org/10.1111/2041-210X.13965> (cf. p. 68)

- STREBEL, N., FISS, C. J., KELLNER, K. F., LARKIN, J. L., KÉRY, M., & COHEN, J. (2021). Estimating abundance based on time-to-detection data. *Methods in Ecology and Evolution*, *n/a(n/a)*. <https://doi.org/10.1111/2041-210X.13570> (cf. p. 57)
- SYKES, J. M., HORRILL, A. D., & MOUNTFORD, M. D. (1983). Use of Visual Cover Assessments as Quantitative Estimators of Some British Woodland Taxa. *Journal of Ecology*, *71*(2), 437-450. <https://doi.org/10.2307/2259726> (cf. p. 57)
- TAY, J. Y. L., ERFMEIER, A., & KALWIJ, J. M. (2018). Reaching new heights : can drones replace current methods to study plant population dynamics? *Plant Ecology*, *219*(10), 1139-1150. <https://doi.org/10.1007/s11258-018-0865-8> (cf. p. 74)
- THOMAS, L., BURNHAM, K. P., & BUCKLAND, S. T. (2004). Temporal inferences from distance sampling surveys. In S. T. BUCKLAND, D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, L. THOMAS, S. T. BUCKLAND, D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE & D. L. BORCHERS (Éd.), *Advanced Distance Sampling : Estimating abundance of biological populations* (p. 71-107). Oxford University Press. (Cf. p. 56).
- THOMPSON, K., & GRIME, J. P. (1979). Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats. *Journal of Ecology*, *67*(3), 893-921. <https://doi.org/10.2307/2259220> (cf. p. 75)
- THOMPSON, S. (1990). Adaptive Cluster Sampling. *Journal of the American Statistical Association*, *85*(412), 1050-1059. <https://doi.org/10.2307/2289601> (cf. p. 46)
- TREURNICHT, M., SCHURR, F. M., SLINGSBY, J. A., ESLER, K. J., & PAGEL, J. (2021). Range-wide population viability analyses reveal high sensitivity to wildflower harvesting in extreme environments. *Journal of Applied Ecology*, *58*(7), 1399-1410. <https://doi.org/10.1111/1365-2664.13882> (cf. p. 59)
- TURK, P., & BORKOWSKI, J. J. (2005). A review of adaptive cluster sampling : 1990–2003. *Environmental and Ecological Statistics*, *12*(1), 55-94. <https://doi.org/10.1007/s10651-005-6818-0> (cf. p. 46)
- TYRE, A. J., TENHUMBERG, B., FIELD, S. A., NIEJALKE, D., PARRIS, K., & POSSINGHAM, H. P. (2003). Improving Precision and Reducing Bias in Biological Surveys : Estimating False-Negative Error Rates. *Ecological Applications*, *13*(6), 1790-1801. <https://doi.org/10.1890/102-5078> (cf. p. 41, 53)
- URQUHART, N. S. (2012). The role of monitoring design in detecting trend in long-term ecological monitoring studies. In A. B. COOPER, D. S. LICHT, J. J. MILLSPAUGH & R. A. GITZEN (Éd.), *Design and Analysis of Long-term Ecological Monitoring Studies* (p. 151-173). Cambridge University Press. <https://doi.org/10.1017/CBO9781139022422.011>. (Cf. p. 45, 48)
- VEECH, J. A., OTT, J. R., & TROY, J. R. (2016). Intrinsic heterogeneity in detection probability and its effect on N-mixture models. *Methods in Ecology and Evolution*, *7*(9), 1019-1028. <https://doi.org/10.1111/2041-210X.12566> (cf. p. 55)
- VITTOZ, P., BAYFIELD, N., BROOKER, R., ELSTON, D. A., DUFF, E. I., THEURILLAT, J.-P., & GUISAN, A. (2010). Reproducibility of species lists, visual cover estimates and frequency methods for recording high-mountain vegetation. *Journal of Vegetation Science*, *21*(6), 1035-1047. <https://doi.org/10.1111/j.1654-1103.2010.01216.x> (cf. p. 57)
- WATSON, J., & ESTES, J. A. (2011). Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological*

- Monographs*, 81(2), 215-239. <https://doi.org/10.1890/10-0262.1> (cf. p. 39)
- WAUCHOPE, H. S., AMANO, T., SUTHERLAND, W. J., & JOHNSTON, A. (2019). When can we trust population trends? A method for quantifying the effects of sampling interval and duration. *Methods in Ecology and Evolution*, 10(12), 2067-2078. <https://doi.org/10.1111/2041-210X.13302> (cf. p. 49)
- WEBSTER, R., WELHAM, S. J., POTTS, J. M., & OLIVER, M. A. (2006). Estimating the spatial scales of regionalized variables by nested sampling, hierarchical analysis of variance and residual maximum likelihood. *Computers & Geosciences*, 32(9), 1320-1333. <https://doi.org/10.1016/j.cageo.2005.12.002> (cf. p. 73)
- WEISER, E. L., DIFFENDORFER, J. E., LOPEZ-HOFFMAN, L., SEMMENS, D., & THOGMARTIN, W. E. (2021). TrendPowerTool : A lookup tool for estimating the statistical power of a monitoring program to detect population trends. *Conservation Science and Practice*, 3(7), e445. <https://doi.org/10.1111/csp2.445> (cf. p. 50)
- WHITE, E. R. (2019). Minimum Time Required to Detect Population Trends : The Need for Long-Term Monitoring Programs. *BioScience*, 69(1), 40-46. <https://doi.org/10.1093/biosci/biy144> (cf. p. 49)
- WILLIAMS, B. K., NICHOLS, J. D., & CONROY, M. J. (2002). *Analysis and Management of Animal Populations : Modeling, Estimation, and Decision Making*. Academic Press. (Cf. p. 39, 41, 43, 63, 67, 68).
- WRIGHT, W. J., IRVINE, K. M., WARREN, J. M., & BARNETT, J. K. (2017). Statistical design and analysis for plant cover studies with multiple sources of observation errors. *Methods in Ecology and Evolution*, 8(12), 1832-1841. <https://doi.org/https://doi.org/10.1111/2041-210X.12825> (cf. p. 53, 58)
- YOCCOZ, N. G., NICHOLS, J. D., & BOULINIER, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16(8), 446-453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4) (cf. p. 39, 40, 42, 43)
- ZIPKIN, E. F., & SAUNDERS, S. P. (2018). Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation*, 217, 240-250. <https://doi.org/10.1016/j.biocon.2017.10.017> (cf. p. 76)



Campanule des Alpes (*Campanula alpina*), massif des Făgăraș, Roumanie, août 2022.

Chapitre 2

Les méthodes d'échantillonnage spatialement équilibrées sont toujours plus précises que les méthodes d'échantillonnage aléatoires pour estimer la taille de populations agrégées

L'objectif du deuxième chapitre de cette thèse est de proposer une manière d'améliorer la précision des estimations de taille de population en adaptant le plan d'échantillonnage au niveau d'agrégation des individus au sein de la population étudiée. Comme cela a été présenté dans le premier chapitre, un des moyens pour estimer la tendance d'une population est d'estimer sa taille de manière répétée au cours du temps en tirant un nouvel échantillon d'unités spatiales à chaque itération. Si les individus sont agrégés dans l'espace comme c'est fréquent dans les populations de plantes, les comptages ont une plus grande variance que pour une population spatialement homogène, et les estimations de taille et de tendance des populations sont moins précises. Afin de déterminer comment améliorer la précision des estimations de taille des populations agrégées, j'ai utilisé des simulations informatiques afin de pouvoir manipuler à volonté les caractéristiques de la population étudiée et du plan d'échantillonnage. Cela m'a permis d'identifier les facteurs les plus importants pour la précision des estimations de taille de population, et de comprendre pourquoi les méthodes d'échantillonnage fournissent parfois des estimations de précision similaire et parfois avec d'importantes différences de précision. Cette étude permet d'apporter un regard nouveau sur les travaux comparant la précision de méthodes d'échantillonnage publiées ces dernières décennies, qui ont parfois conclu que la méthode d'échantillonnage n'avait pas d'influence majeure sur la précision des estimations et parfois l'inverse. Cette situation empêchait de donner des recommandations claires sur la manière d'adapter les plans d'échantillonnage à l'agrégation des individus, et a pu être en partie résolue grâce à la présente étude. Afin de vérifier que les résultats des simulations étaient bien transposables au réel, j'ai comparé la précision des trois méthodes d'échantillonnage sur trois populations de plantes ayant des niveaux d'agrégation contrastés. Les niveaux de précision des estimations étaient similaires sur les populations réelles et les populations simulées, confirmant ainsi la validité des résultats dans le monde réel.

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Spatially balanced sampling methods are always more precise than random ones for estimating the size of aggregated populations

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Abstract

1. Population size is a crucial parameter for both ecological research and conservation planning. When individuals are aggregated, estimating the size of a population through sampling raises methodological challenges, as the high variance between sampling units leads to imprecise estimates. Choosing the right sample design depending on the population aggregation level could improve the precision of estimates ; however, this is difficult because studies comparing sample designs for aggregated populations have been limited to a few populations and sampling designs, so their results cannot be generalised.
2. To address this gap, we combined simulations of spatial point populations and field counts of three plant species to compare the relative precision of estimates between three sampling methods : simple random sampling (SRS), systematic sampling (SYS), and spatially balanced sampling (SBS). Comparisons were performed on density and aggregation gradients for a range of sample sizes.
3. Our simulations showed that SYS and SBS were always more precise than SRS when individuals were aggregated, reducing sampling variance up to 80% and 60%. The highest precision for estimating population size was always obtained when the average distance between sampling units equalled the diameter of the clusters (i.e. the groups of individuals). The difference in precision was similar for the natural populations, with sampling variance lowered by up to 75% (SYS) and 60% (SBS) compared to SRS.
4. These findings lead us to recommend using SYS or SBS rather than SRS to estimate population size when individuals are spatially aggregated, as these consistently provide more precise estimates. Assessing cluster diameters in the field enables a quick assessment of the potential gain in precision to expect, and thus the best choice of sampling method depending on the trade-off between precision and field constraints.

Keywords— survey design - sampling error - population monitoring - plant population - clustered population - autocorrelation - spatial point process - balanced acceptance sampling

2.1 Introduction

Population size is a central parameter for all fields related to ecology and evolution. Evolutionary biologists use population size to predict the risk of genetic diversity loss due to inbreeding and genetic drift (CROW, 2010; FRANKHAM, 1995). Ecologists study how population size varies over space and time to identify biotic interactions and abiotic factors that shape population dynamics (BJØRNSTAD & GRENFELL, 2001; QUÉROUÉ et al., 2021) and their possible cascading consequences on ecosystems, as in biological invasions (SIMBERLOFF et al., 2013) or the reintroduction of keystone species (RIPPLE & BESCHTA, 2012; WATSON & ESTES, 2011). In conservation biology, population size is used to assess extinction risk (DENNIS et al., 1991) and species conservation status (e.g. IUCN, 2019) and to evaluate the effectiveness of management actions (BEISSINGER & MCCULLOUGH, 2002). Despite its apparent simplicity, estimating the size of a population raises several methodological challenges, as it is often impossible to count every individual. Ecologists thus rely on sampling : counting individuals in a subset of spatial units occupied by the studied population to infer the entire population size (COCHRAN, 1977).

Sampling is a prolific field of statistics, and various methods exist for selecting sampling units (THOMPSON, 2012). Whatever the sampling method, estimating the size of a population denoted Y is achieved through the same four steps (COCHRAN, 1977) : (1) Defining a statistical population made up of N units, usually spatial units (e.g. all possible quadrats covering the study area); (2) Drawing from this a sample of n units on which to conduct counts of individuals, denoted y_1, y_2, \dots, y_n ; (3) Estimating the mean number of individuals per unit as the sample mean $\hat{Y} = \bar{y} = \frac{1}{n} \sum_{i=1}^n y_i$; finally (4) Inferring the entire population size by multiplying the sample mean by the number of sampling units in the statistical population $\hat{Y} = N\bar{y}$. The precision of the density estimate \hat{Y} depends on the sample size n , higher sample sizes reducing the sampling variance, and on two population parameters : the population mean \bar{Y} , and the dispersion of the number of individuals per sampling unit y_i around the mean. A higher population mean tends to increase the sampling variance. For a population with a given mean number of individuals per sampling unit, the more heterogeneous these numbers between units, the less precise the estimates of the mean number of individuals per sampling unit

(COCHRAN, 1977). Therefore, the distribution of individuals in the studied population strongly affects the precision of the estimates.

In natural populations, individuals are usually not randomly distributed in space (LEGENDRE, 1993; LEVIN, 1992). Distribution may indicate a process of repulsion, with individuals more distant from their nearest neighbours than expected in a random distribution. Repulsion can occur, for example, in territorial animals (e.g. HINDE, 1956; MAHER & LOTT, 2000) or in plant species due to intra-specific (STOLL & BERGIUS, 2005) or interspecific competition (RAYBURN & SCHUPP, 2013). When sampling such populations, the number of individuals per sampling unit is relatively homogeneous, so population density estimates have a high precision even with relatively small sample sizes (COCHRAN, 1977). Alternatively, individuals may aggregate, living closer to their nearest neighbours than expected in a random distribution (hereafter referred to as “aggregated populations”). Aggregation of individuals is frequent in herbaceous plant species, leading many authors to state that most plant populations are aggregated (DAMGAARD & IRVINE, 2019; GREIG-SMITH, 1983; ROBINSON, 1954). This arises due to limited dispersal capacity or a patchy habitat (LARA-ROMERO et al., 2016; SEABLOOM et al., 2005). Aggregation can also be observed in animals, such as colonial breeding vertebrates (DANCHIN & WAGNER, 1997) and freshwater mussels (MORALES et al., 2006; SMITH et al., 2011). When sampling aggregated populations, samples are typically composed of many zeros and a few high counts, resulting in imprecise estimates (MCGARVEY et al., 2016). This makes improving the precision of population size estimates for aggregated populations by choosing an appropriate sampling design an important challenge (THOMPSON, 2004; YOCCOZ et al., 2001).

Two types of sampling methods can be used for aggregated populations : one-step methods, in which all sampling units are selected prior to measurements in the field, and two-step methods, in which a sample of primary units is selected and counted in the field, and new units are added depending on the outcome of counts on primary units. Adaptive cluster sampling (ACS; THOMPSON, 1990) is a two-step method specifically developed for aggregated populations. Although it usually improves the precision of population size estimates (TURK & BORKOWSKI, 2005), it is difficult to implement in the field (see, however, MORRISON et al., 2008; PHILIPPI, 2005) and can lead to

very uncertain estimates for small or very aggregated populations (SHACKLETON et al., 2020), so we did not cover it in this study. The most commonly used one-step sampling methods (SMITH et al., 2017) are simple random sampling (SRS), in which the units are randomly selected, and systematic sampling (SYS), in which the location of the first unit is randomly selected and the others are arranged along a rectangular grid (COCHRAN, 1977). Spatially balanced sampling (SBS) is a more recent one-step sampling method in which selected units are evenly distributed over the study area but without imposing a strictly equal distance between units as in SYS. This can be done through various processes, such as dividing the study area into multiple spatial strata and selecting one unit from each (STEVENS & OLSEN, 2004) or using a random-start low-discrepancy sequence to select the location of the sampling units (ROBERTSON et al., 2013). These sampling methods yield varyingly precise estimates depending on the spatial distribution of individuals in the studied population (MCGARVEY et al., 2016). However, no clear guidelines have yet been proposed on the best sampling method to choose depending on the observed aggregation.

To date, three types of studies have provided information about the relative precision of sampling methods for aggregated populations :

1. Some compare the precision of estimates between sampling methods in a purely analytical way : for example, they showed that SYS is more precise than SRS for populations with certain types of autocorrelation in the density of individuals (COCHRAN, 1946; COCHRAN, 1977; MATÉRN, 1986; QUENOUILLE, 1949). However, since the autocorrelation of density is generally unknown prior to fieldwork, these conclusions are difficult to translate into operational recommendations.
2. Some map all individuals from a given population in the field and simulate multiple sampling designs on the raw data or simulated populations with similar characteristics. This approach is valuable in identifying the sampling methods that provide the most precise estimates for a given population but lacks generality, especially as the conclusions about the relative precision of the sampling methods vary between studies. Indeed, SYS or SBS are often found to be more precise than SRS, but the difference in precision varies considerably between stu-

dies (KERMORVANT et al., 2020; MIER & PICQUELLE, 2008; MORRISON et al., 2008), and a non-negligible fraction of the studies find all sampling methods to yield roughly the same precision (KHAEMBA et al., 2001; SMITH et al., 2011). However, to our knowledge, no study has found SRS to be more precise than SYS or SBS.

3. Some simulate virtual populations with various spatial distributions on which they then simulate multiple sampling designs. For example, MCGARVEY et al. (2016) simulated populations with multiple levels of aggregation and explored how the precision of estimates varied between SRS and SYS for a sample size of $n = 100$. They found that SYS was substantially more precise than SRS for all aggregated populations.

The three types of studies seem to indicate that SYS and SBS usually yield more or as precise estimates than SRS. However, it is unclear which method between SYS and SBS yields the most precise estimates, and no previous study has described how the relative precision of the sampling methods varies as a function of the three parameters affecting the precision of estimates : the mean density of individuals, their aggregation level and sample size. Furthermore, it has been shown analytically that SYS provides more precise estimates than SRS if the variance within the systematic samples is higher than the variance of the whole population (COCHRAN, 1977, p.208). However, the mechanism determining the within-sample variance, and thus the precision of SYS relatively to SRS, has never been described. Understanding this mechanism would allow knowing with certainty which is the optimal sampling design for any studied population.

This study aimed to determine which sampling method provides the most precise estimates depending on the level of aggregation of the population. To this end, we combined computer-based simulations and field counts of plant populations to compare the precision of three one-step sampling methods (SRS, SYS and SBS) over wide gradients of density, aggregation and sample size. We sought to answer four key questions : (i) Does aggregation have the same effect on estimate precision across the three sampling methods? (ii) Does the effect of aggregation on estimate precision change with population density? (iii) Does the effect of aggregation on estimate precision change with

sample size? (iv) What is the mechanism generating the differences in precision between sampling methods for aggregated populations?

2.2 Materials and methods

Our simulations followed a three-step procedure : (1) we generated virtual populations for a given combination of density and aggregation, (2) we drew samples from each virtual population with three sampling methods (SRS, SYS and SBS) and several sample sizes, and (3), we measured the precision of the density estimates obtained with each sampling method and sample size for each virtual population (Fig. 2.1).

2.2.1 Simulation of the virtual populations

We generated virtual populations by simulating spatial point patterns in which each point represented the location of an individual of the population of interest. We simulated the populations inside a study area of 100x100 spatial units (i.e. as the dimensions were virtual, they could be any surface area), and the sampling units were all 10,000 spatial units (hereafter called “cells”) with a dimension of 1x1 covering the study area. The distribution of individuals was generated using point process models (BADDELEY et al., 2015). We investigated an aggregation gradient ranging from (i) populations in which individuals repel each other, (ii) to randomly located individuals, (iii) to populations in which individuals aggregate. We thus used three different point process models to generate the populations.

We simulated populations with randomly located individuals using a Poisson point process, in which point locations are determined by randomly drawing their x and y coordinates. We simulated populations with repulsion between individuals using a simple sequential inhibition (SSI) process. In this point process, randomly located points are added one by one to the study area, and if a point falls closer than a chosen distance r from an existing point, it is deleted, and a new random point is generated (BADDELEY et al., 2015). Lastly, we simulated populations with individuals aggregating into clusters (i.e. circular groups of individuals) using a Matérn cluster process. This consists of four steps : (1) a set of “parent” points is generated using a Poisson point process with a mean density denoted κ ; (2) a disc of a given radius, denoted $scale$, is centred on

each parent point ; (3) “offspring” points are distributed across each disc using a Poisson point process with a mean density noted μ ; (4) parent points are then suppressed from the simulated distribution. The clusters can overlap, leading to areas with a high point density (MATÉRN, 1986). The mean density of the individuals is $\lambda = \text{kappa} * \mu$, and scale only modulates the surface area of the clusters. Therefore, when simulating point patterns with a Matérn cluster process, the density of individuals can be increased by increasing only kappa , only μ , or kappa and μ simultaneously. These three ways to increase density result in populations with different spatial structures, i.e. populations with more clusters, clusters with more individuals, or both. As this could affect the precision of density estimates, we simulated all combinations of density and aggregation (as defined below) using the three approaches. For populations in which kappa and μ increased simultaneously (modality 1), we kept the ratio of μ over kappa at 10,000. For populations in which only kappa was increased (modality 2), μ was kept constant at 100 individuals/cluster. For populations in which only μ was increased (modality 3), kappa was kept at 0.01 clusters/cell.

In order to compare the populations simulated with the three types of point processes (Poisson, SSI and Matérn cluster), we used the index of dispersion I as a common metric of aggregation. This index is defined as σ^2 / \bar{Y} , where \bar{Y} is the mean density of individuals in every possible cell of the study area, and σ^2 is the associated variance. I is equal to one for populations with randomly distributed individuals, decreases when individuals show repulsion (its minimum possible value being 0) and increases when individuals aggregate (with no upper bound; BADDELEY et al., 2015, p.201). For the populations simulated with the Matérn cluster process, we had to increase the cluster radius when increasing population density to maintain the same value of dispersion index in modalities 1 and 3. Thus, populations with the same dispersion index had larger clusters as density increased, except for modality 2, in which clusters had the same radius for the same level of dispersion index at all densities (Appendix 1).

We chose the extent of the density and aggregation gradients based on our knowledge of plant ecology and published literature (see, for example, GREIG-SMITH, 1983 ; MORRISON et al., 2008 ; REISCH et al., 2018). Thus, we simulated populations with seven densities (1, 5, 10, 15, 20, 25 and 30 individuals/cell) and 78 different aggregation

levels ($I = 0.4, 0.6$ and 0.8 with the SSI process; $I = 1$ with the Poisson process; $I =$ from 2 to 75 with the Matérn cluster process). We simulated all aggregation levels for all densities, except those generated with the SSI process, which we simulated only for densities of 1, 10 and 20 individuals/cell to save computation time. Altogether, we simulated populations for 534 combinations of density and aggregation, and for each combination we simulated 60 populations. Examples of these populations can be found in Appendix 2.

2.2.2 Sampling process

We selected nine sample sizes : $n = 9, 15, 25, 49, 100, 150, 196, 300$ and 400 (out of 10,000 possible sample units) because for systematic sampling they allow the sample units to be arranged in a square or quasi-square grid, which limits major spatial coverage differences between sample sizes. Many ways of performing spatially balanced sampling have been proposed, and we chose one of the most commonly used, called Balanced Acceptance Sampling (BAS), in which the sampling units are selected by drawing their coordinates from a low discrepancy sequence, in our case the Halton sequence (ROBERTSON et al., 2013). BAS is one of the methods yielding the best spatial balance when all units are accepted, which was always the case in our simulations (ROBERTSON et al., 2018). For each virtual population, we simulated 1,000 sampling surveys for each of the nine sample sizes. A survey consisted of two steps : drawing a sample of size n from a population with each of the three sampling methods and storing the mean densities calculated from the three samples. For SYS and SRS, all sampling units have the same inclusion probability, thus the sample mean is an unbiased estimator of the population mean density (COCHRAN, 1977). For SBS as we simulated it, inclusion probabilities are equal to the 3rd or 4th decimal (ROBERTSON et al., 2013), so we treated them as equiprobable, as weighting the sample mean by the inclusion probability of the units would have had no discernible effect on our results. Altogether, we simulated 60,000 sampling surveys by combination of density, aggregation and sample size, i.e. 1,000 sampling surveys on 60 virtual populations.

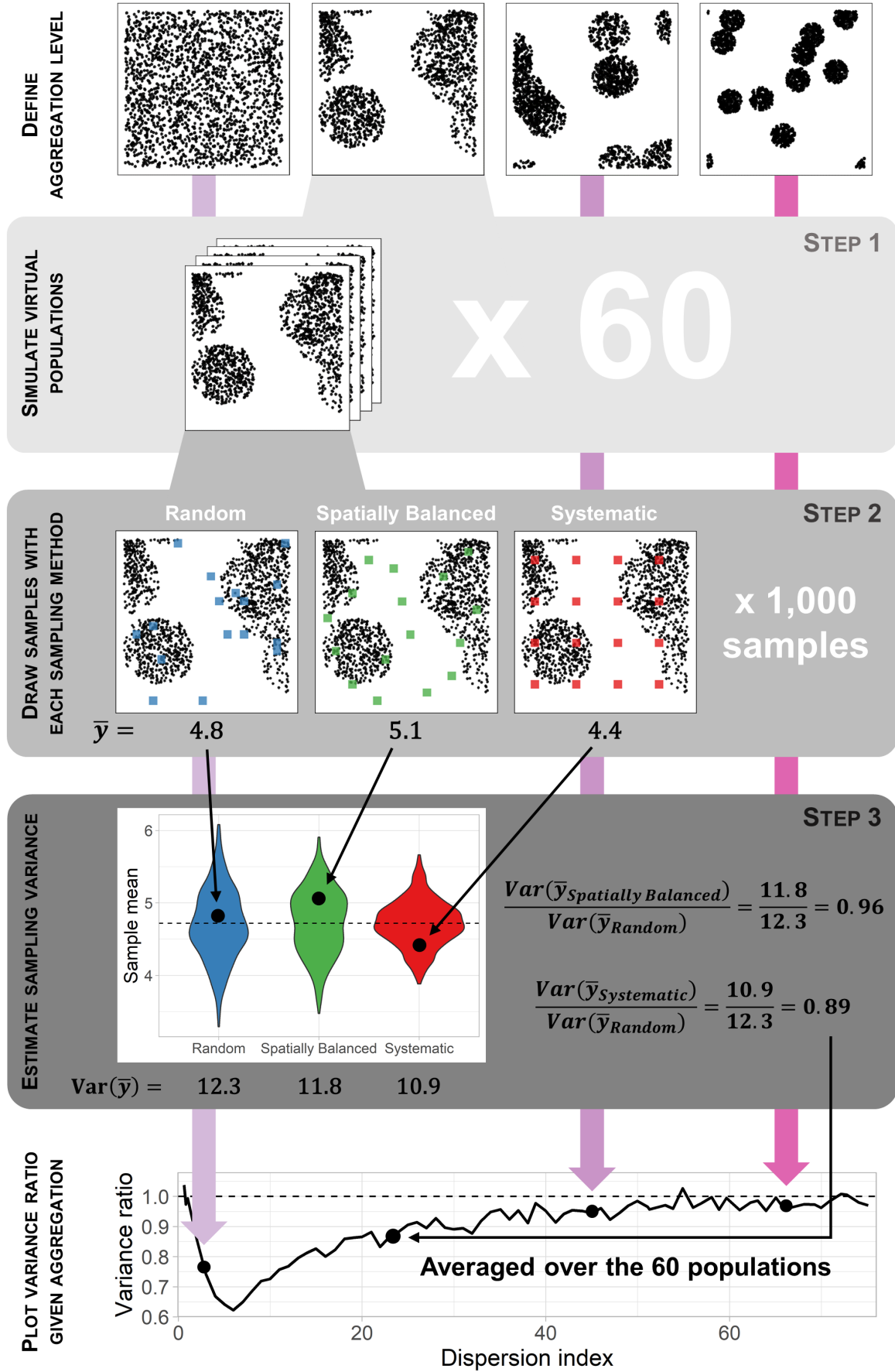


FIGURE 2.1 – Workflow of the simulation process. One level of density (out of seven) and four levels of aggregation (out of 78) are represented. The simulation process is described for one aggregation level and one sample size (out of nine). For every level of aggregation (top row), we simulated 60 virtual populations (Step 1). We drew 1,000 samples of size n with each of the three sampling methods from every population and computed their means (Step 2). We calculated the variance of the 1,000 sample means to estimate the sampling variance and computed the ratios of the sampling variance of systematic sampling (SYS) and spatially balanced sampling (SBS) relative to simple random sampling (SRS; Step 3). The horizontal dotted line on the violin plot represents the true mean density of the sampled population. The final result is the curve of the variance ratio as a function of the population aggregation level, each point of the curve being the average over 60 virtual populations. For clarity, only the curve for $\text{Var}(\text{Systematic})/\text{Var}(\text{Random})$ is shown.

2.2.3 Comparison of estimate precision between sampling methods

Before comparing the precision of the density estimates obtained with each sampling method, we first checked if they were unbiased. Then, for each combination of density, aggregation and sample size, we computed the mean of the 1,000 mean densities calculated from the samples for each of the 60 virtual populations. We then averaged the resulting 60 mean densities and compared the result to the mean of the true densities of the 60 virtual populations that were sampled. The estimated density was always very close to the true density (see Appendix 3), indicating that the estimates obtained with the three sampling methods were unbiased, as expected from sampling theory (THOMPSON, 2012).

To measure the precision of the density estimates, we estimated the sampling variance for every combination of sampling method and sample size by computing the variance of the means of the 1,000 corresponding sampling surveys for each virtual population. This method of estimating the sampling variance avoids the need for variance estimators, but requires knowing the mean of all possible samples (although in our case we did not draw all possible samples but a large proportion of them) and can therefore only be used in simulation studies (MAGNUSSEN & FEHRMANN, 2019; MAGNUSSEN et al., 2020; MCGARVEY et al., 2016). This method allows to estimate the conditional sampling variance, i.e. conditional on a realised population covering a finite area as encountered in the field, within the context of design-based inference (see BRUS (2021) for a synthesis on design-based and model-based inference). To compare the estimate

precision between the three sampling methods for a given sample size, we calculated the ratio of the sampling variance of SYS and SBS, relative to the sampling variance of SRS. This indicator represents the rate of reduction in variance obtained on average when changing from SRS to another sampling method (KISH, 1965). A variance ratio below one means that a method (here SYS or SBS) is more precise than SRS. The variance ratio can also be interpreted as the effective sample size (KISH, 1965). Its inverse then represents the rate of increase in sample size required to achieve the same precision as the alternative method using SRS. For example, for a sample size of $n = 100$, a ratio of 0.5 between the sampling variance of SYS and SRS means that SRS would need, on average, a sample size of $n = 100 \cdot (1/0.5) = 200$ to achieve the same precision as SYS with $n = 100$. To obtain a generalisable result, for each sample size, we averaged the variance ratio values over the 60 virtual populations that were sampled for each combination of density and aggregation. Hence, the values of variance ratio we present are the expected values for each combination of density, aggregation and sample size (MAGNUSSEN et al., 2020).

2.2.4 Field study

To compare our results from simulated populations with natural populations, we conducted a field survey to map the distribution of all individuals in one population for three herbaceous plant species exhibiting different levels of density and aggregation. We chose a population of *Bellis sylvestris* Cirillo, a common Mediterranean Asteraceae, to illustrate a population with approximately randomly distributed individuals; a population of *Sanguisorba minor* L., a Rosaceae common in the Mediterranean basin, to illustrate a population with high density and slightly aggregated individuals; and a population of *Limonium girardianum* Guss. to illustrate a population in which individuals are highly aggregated and form well-delimited clusters – this Plumbaginaceae is endemic in the northwest Mediterranean basin and grows in saltmarshes on small sand mounds a few metres wide.

To survey these populations, we placed a 20x20 m square on each and mapped all individuals in each 10x10 cm cell using 1x1 m quadrats subdivided with a 100-cell grid. To analyse the data from the three natural populations, we grouped the cells four by four to obtain the total number of individuals per 20x20 cm cell to have a study

area of 100x100 cells as for the virtual populations. We simulated the same sampling surveys on the counts of the three natural populations as on the virtual populations and computed the variance ratio of SYS and SBS relative to SRS. In order to test whether cluster diameter can be quickly assessed in the field, an observer surveyed the study area by splitting the 20x20 m square into 20 columns 1 m in width. He then walked through every second column and measured the largest width of five randomly selected clusters intersected by the column.

All the simulations were performed in R version 3.6.1 (R CORE TEAM, 2019). The spatial point patterns were generated with the package spatstat (BADDELEY et al., 2015). The functions used to draw the samples were either programmed by the authors or adapted from the package SDraw (MCDONALD & MCDONALD, 2020).

2.3 Results

2.3.1 Comparison of estimate precision between the three sampling methods for the virtual populations

The relative precision of the three sampling methods varied considerably with the aggregation level (Fig. 2.2). For randomly distributed populations ($I=1$) and populations exhibiting repulsion ($I<1$), the values of the variance ratio were close to one : i.e. SRS, SBS and SYS had equivalent precision. This result was consistent for all densities and sample sizes tested. For all populations with aggregated individuals ($I>1$), whatever the sample size, SYS and SBS were always as precise or more precise than SRS, and SYS was always more precise than SBS. For both SYS and SBS, the variance ratio decreased rapidly below one as aggregation increased, and after reaching a minimum, it slowly increased towards 1. This means that as the aggregation of individuals increased, the estimates obtained with SYS and SBS quickly became more precise than those obtained with SRS until they reached a maximum of relative precision. After this maximum, their relative precision slowly decreased until it became equivalent to SRS for high aggregation levels. When the sample size was increased, the minimum of the variance ratio had a lower value and shifted towards higher levels of aggregation. In other words, as sample size increased, SYS and SBS became increasingly more precise than SRS,

and maximum relative precision was reached at higher aggregation levels.

The effect of the mean density depended on the modality we used to simulate increasing density. For modality 1 (shown in Fig. 2.2), when density increased, the variance ratio had lower values, and its minimum shifted towards higher aggregation levels. In other words, as density increased, SYS and SBS became more precise relative to SRS, and their maximum relative precision shifted towards more aggregated populations. For modality 3, the same pattern occurred in a more pronounced way. In contrast, for modality 2, the variance ratio curves were identical for all densities (Appendix 1). These modalities differed in that the diameter of the clusters changed with density for modalities 1 and 3, but not for modality 2. Therefore, cluster diameter appeared central to explain the relative precision of the sampling methods.

To investigate this result, we represented the variance ratio as a function of the diameter of clusters instead of the dispersion index. Figure 2.3 shows that the relative precision of SYS compared to SRS for a given sample size was the same for all densities and depended only on cluster diameter. Moreover, the variance ratio only reached one when the cluster diameter was so small that clusters could fit in one sampling unit. We obtained the same result for SBS (Appendix 1) and for all populations, regardless of the modality used to simulate increasing density. Furthermore, the minimum variance ratio of SYS and SBS was always reached when the mean distance between the sampling units was equal to the cluster diameter.

2.3.2 Relative precision of estimates for three plant populations

The *B. sylvestris* population had a mean density of 0.079 individual per 20x20 cm cell and a dispersion index of 2.87. Individuals were thus slightly aggregated, although it was difficult to clearly distinguish clusters (Fig. 2.4). The *S. minor* population had a mean density of 1.47 individuals/cell and a dispersion index of 7.63. Individuals formed clusters of various diameters with indistinct boundaries. The population of *L. girardianum* had a mean density of 1.66 individuals/cell and a dispersion index of 8.42. Individuals were grouped into clusters with clear boundaries, corresponding to the sand mounds present in the study area. For *B. sylvestris*, the cluster diameters measured in the field were within the range [20 cm; 110 cm] with a median of 45 cm; for *S. mi-*

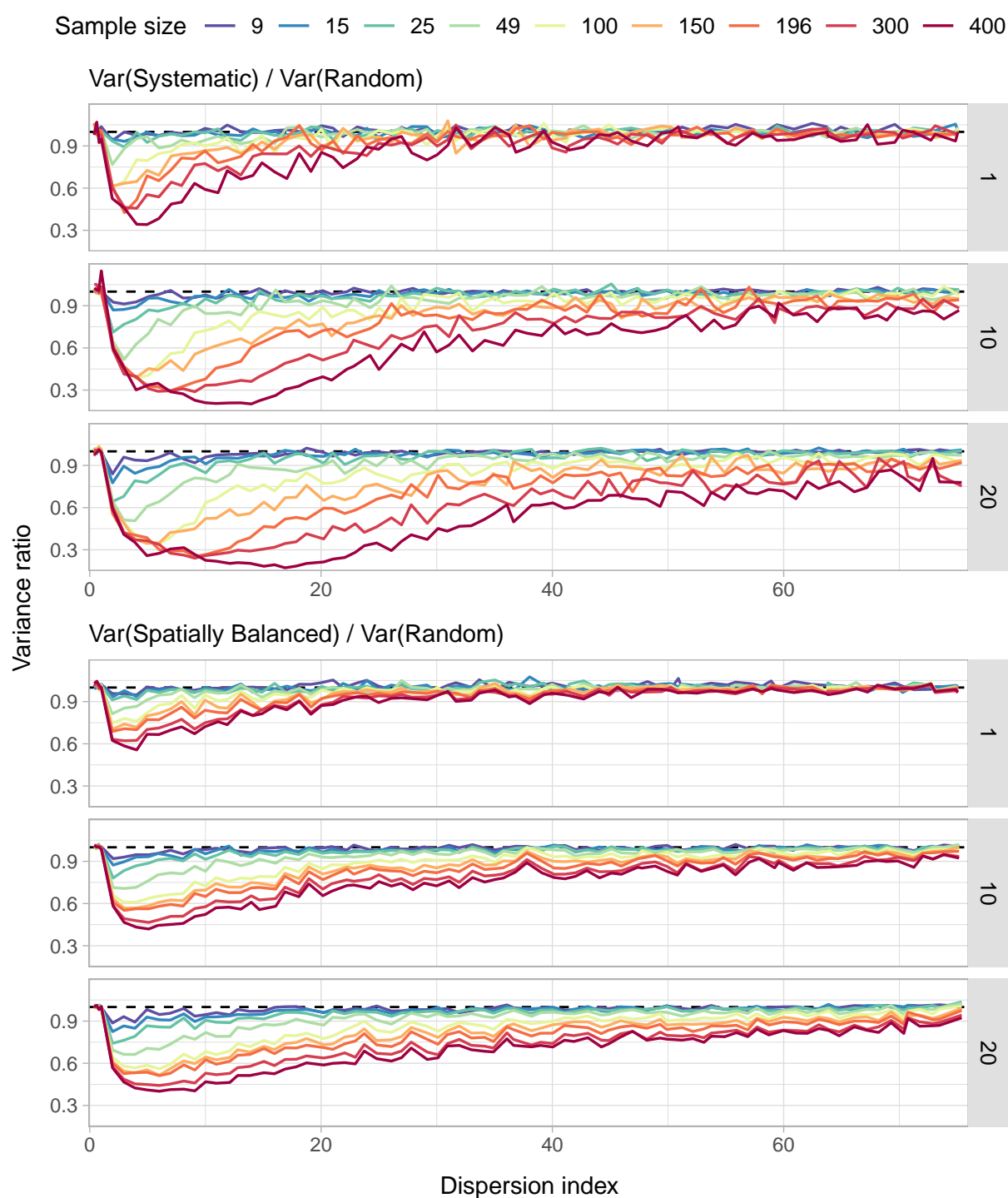


FIGURE 2.2 – Ratio of sampling variance of systematic sampling (SYS) and spatially balanced sampling (SBS) over sampling variance of simple random sampling (SRS), as a function of the dispersion index (I) of the sampled populations. Panels show three mean densities (1, 10 and 20 individuals/cell). For the aggregated populations, density was increased by simultaneously increasing the number of clusters and the number of individuals per cluster (modality 1). Each point of the curves is the ratio of two sampling variances, each estimated from 60,000 sampling survey simulations (1,000 for 60 populations).

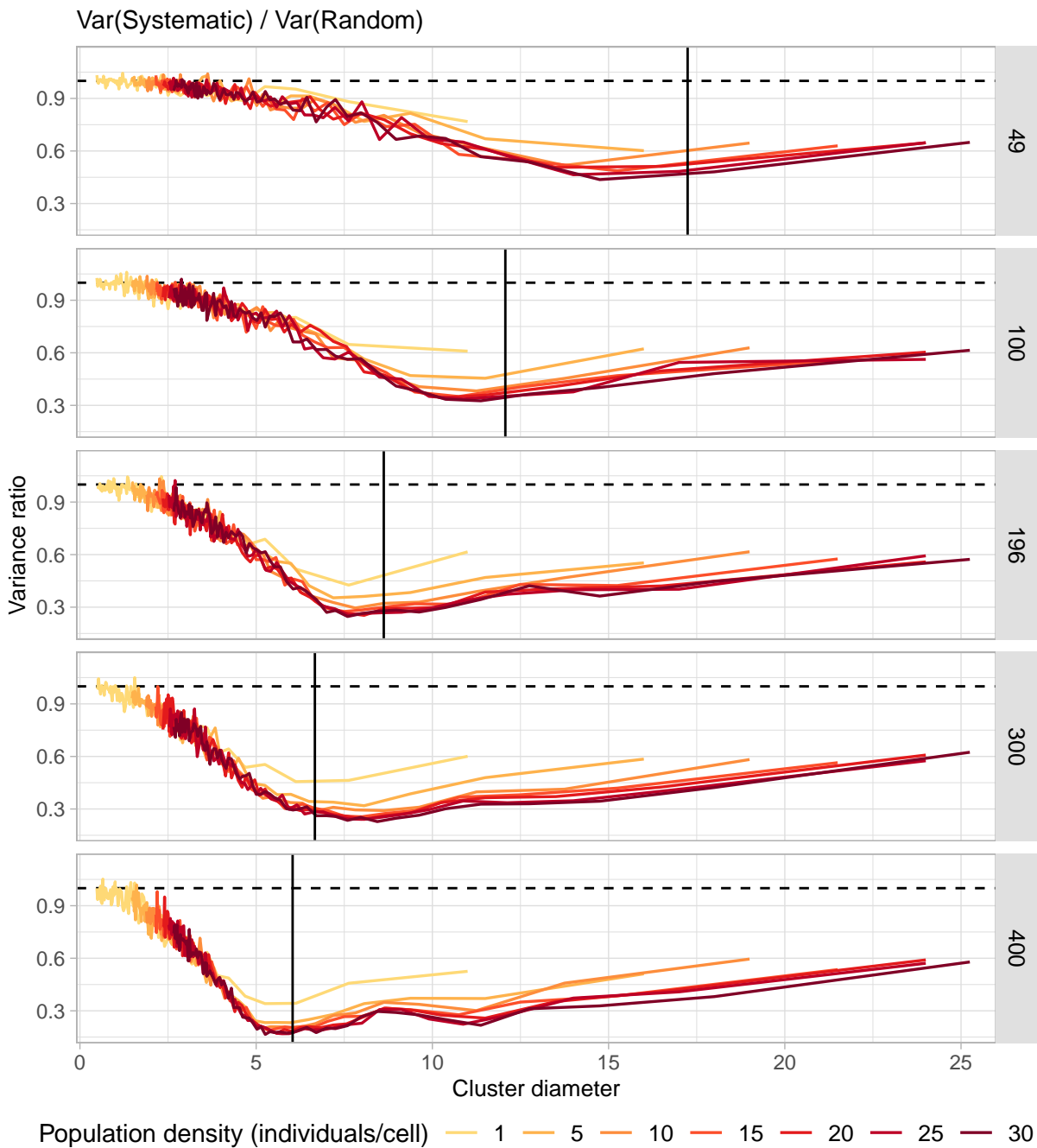


FIGURE 2.3 – Ratio of sampling variance of systematic sampling (SYS) over sampling variance of simple random sampling (SRS) for the aggregated populations. The x-axis is the cluster diameter, and the panels show five different sample sizes. Each curve shows the variance ratio obtained for a given mean density of individuals (from 1 to 30 individuals/cell). The black vertical lines indicate where the distance between the sampling units for SYS is equal to the cluster diameter.

nor, they were within the range [60 cm ; 290 cm] with a median of 145 cm ; and for *L. girardianum* they were within the range [20 cm ; 520 cm] with a median of 90 cm.

For the three populations, the variance ratio was below 1 for both SYS and SBS for almost all sample sizes, indicating that density estimates obtained with SYS and SBS were generally more precise than those obtained with SRS (Fig. 2.4). The variance ratios decreased overall as the sample size increased. The minimum values reached by the variance ratio (0.25 for SYS and 0.40 for SBS) imply that the sample size would have to be increased by 400% and 250% to achieve the same precision as SYS or SBS using SRS. The SYS and SBS methods did not reach their highest relative precision at the point where the mean distance between the sampling units was equal to the median cluster diameter, as was the case for the virtual populations. However, at this point, SYS and SBS were considerably more precise than SRS.

2.4 Discussion

Our findings provide evidence that different one-step sampling methods do not yield estimates of the same precision when estimating the size of aggregated populations. Our simulations showed that this difference in precision depends on the aggregation level of individuals and sample size. For populations of individuals aggregated in clusters of equal diameter, SYS is on average always as or more precise than SBS, which is always as or more precise than SRS for a given sample size. For the virtual populations, sampling variance obtained with SYS and SBS was respectively up to 80% and 60% lower than that obtained with SRS. The difference in precision was similar for the natural populations, with sampling variance up to 75% lower for SYS and 60% lower for SBS compared to SRS. In other words, the fieldwork effort required to estimate population size could be divided by four or five without altering the precision of the final estimates if the sampling design is well calibrated to the aggregation level of the population.

The overall result that SYS is more precise than SRS for aggregated populations is in line with theoretical work (MATÉRN, 1986; QUENOUILLE, 1949) and previous simulation studies (MCGARVEY et al., 2016). Our results show that this holds true for a wide range of population densities, aggregations and sample sizes. The magnitude of

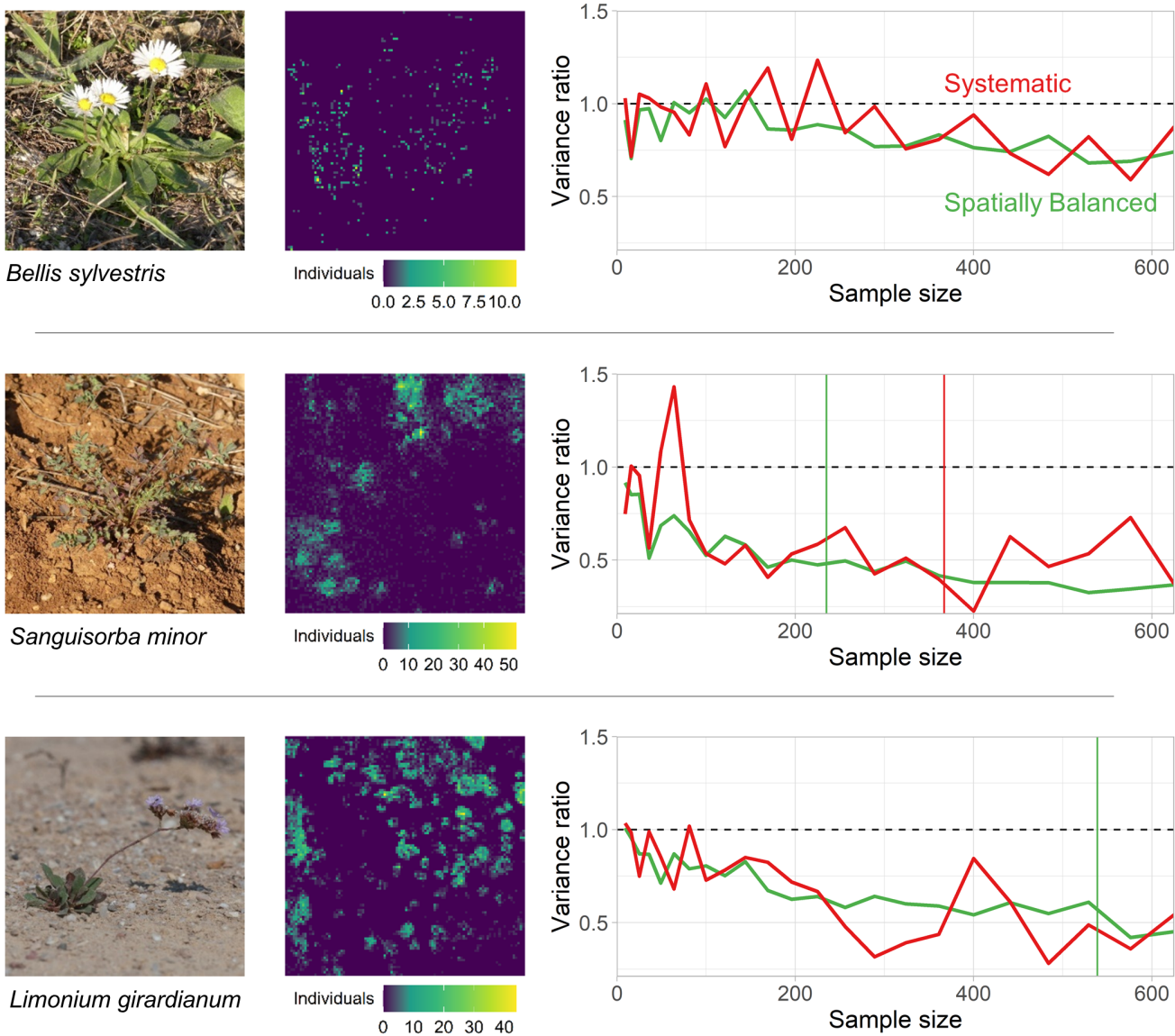


FIGURE 2.4 – Pictures of the three plant species in their natural habitat (left panel), maps of the number of individuals in every 20 x 20 cm cell covering the study area (middle panel) and curves of the ratios $\text{Var}(\text{Systematic})/\text{Var}(\text{Random})$ in red and $\text{Var}(\text{Spatially Balanced})/\text{Var}(\text{Random})$ in green, as a function of sample size (right panel). The vertical lines represent where the mean distance between the sampling units equals the median cluster diameter we measured in the field. For *B. sylvestris*, this exceeds the extent of the sample size gradient shown here. The maximum simulated sample size for the virtual populations was $n = 400$, but here we simulated sample sizes up to $n = 625$ for illustrative purposes.

difference in precision we found in our simulations is consistent with several previous studies (AMBROSIO et al., 2004; MIER & PICQUELLE, 2008; MORRISON et al., 2008), especially regarding the largest differences in precision that were found. For example, MCGARVEY et al. (2016) found a reduction in sampling variance of up to 82% for SYS compared to SRS, and COCHRAN (1977, p. 223) reported studies finding up to 83% lower variance for SYS compared to stratified random sampling. SBS has been less investigated, but the existing simulation studies have also shown that it is usually more precise than SRS (see KERMORVANT et al., 2019, for a summary). Our findings demonstrate that this is true for a large variety of aggregated populations and sample sizes.

2.4.1 How the distribution of individuals drives sampling variance in the virtual populations

Simulating sampling surveys over gradients of population density, aggregation and sample size showed that the relative precision of the sampling methods always followed the same pattern as aggregation increased. Changing the population density and sample size modulated this general pattern, shifting the minimum variance ratio to a higher level of aggregation and lowering its value. Nevertheless, the highest relative precision for SYS and SBS was always achieved when the mean distance between the sampling units was equal to the cluster diameter, whatever the density of individuals (Fig. 2.3). This is because the aggregated populations we simulated were constituted of clusters with the same diameter and number of individuals. In this setup, sampling units located in clusters have values close to each other, and all sampling units located outside clusters are equal to zero. Thus, the sampling variance mainly depends on the between-sample variability in the proportion of sampling units located within clusters. The closer this proportion is between samples, the lower the sampling variance. With SYS and SBS, the spacing between units (fixed for SYS and slightly variable for SBS) leads the proportion of units located in clusters to be less variable between samples than with SRS (Fig. 2.5). Therefore, SYS and SBS will always lead to more precise estimates than SRS, except if the clusters are smaller than the sampling units, in which case all sampling methods will achieve the same precision.

With SYS, when the distance between the sampling units is equal to the cluster diameter (Fig. 2.5, 4th column), all clusters are intersected by a single sampling unit so that the proportion of units located in clusters is strictly identical for all samples. Consequently, the means are very close for all samples, and SYS reaches its optimal precision relative to SRS. When the distance between units is smaller or greater than the cluster diameter, the proportion of units located in clusters is not strictly identical between samples, and the relative precision deviates from the optimum. Using the formulation of COCHRAN (1977, p. 208), for any aggregated population, the within-sample variance is the highest for SYS when the distance between the sampling units is equal to the cluster diameter, and thereby SYS achieves its highest precision relative to SRS. The same mechanism operates for SBS, but as the distance between sampling units is not strictly constant, the proportion of sampling units located in clusters varies more between samples than in SYS. The SBS method is consequently less efficient than SYS for the virtual populations we simulated. Although it has often been stated that sampling methods with better spatial coverage are usually more precise for spatially structured populations (KERMORVANT et al., 2019; ROBERTSON et al., 2013; STEVENS & OLSEN, 2004), the mechanism driving this expectation has, to our knowledge, never been reported before. This mechanism certainly determines the relative precision of all one-step sampling methods when sampling aggregated populations, not only that of the versions of SYS and SBS that we investigated in this study (systematic square-grid sampling and balanced acceptance sampling, respectively).

2.4.2 From computer simulations to field studies

The aggregated populations we simulated had a simplistic spatial structure, as clusters were discs of equal diameter with clear boundaries and containing the same number of individuals. The three plant populations we exhaustively mapped illustrate how natural populations are far less simplistic (Fig. 2.4). In the population of *B. sylvestris*, individuals appeared to be slightly aggregated, but no clear cluster could be identified. The two other populations showed clusters of varying size, with indistinct boundaries, and the distribution of individuals within clusters was heterogeneous. Despite these differences between the virtual and natural populations, the general result that SYS and SBS are more precise than SRS on aggregated populations held true for the three natural po-

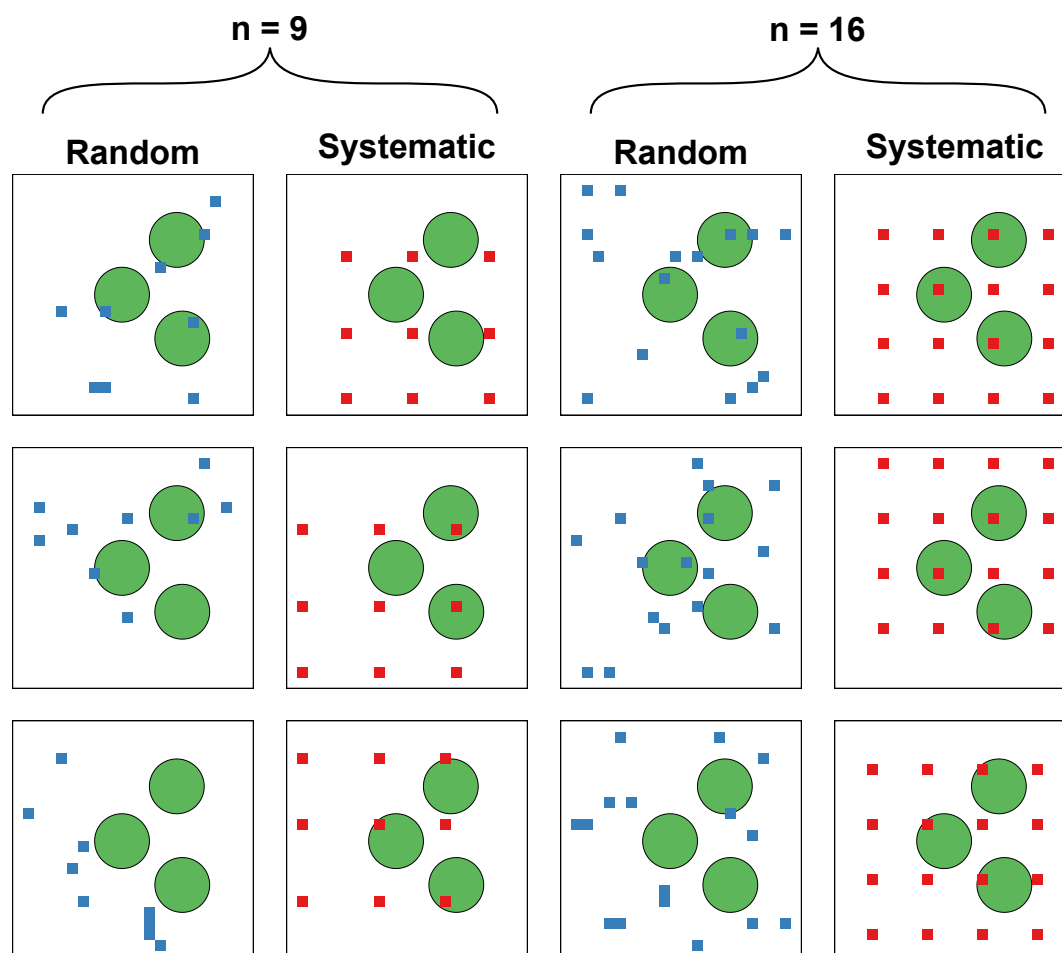


FIGURE 2.5 – Illustration of the mechanism underlying the simulation results regarding the impact of the distance between sampling units on the relative precision of the sampling methods. Three samples drawn from the same virtual population are presented for random (SRS) and systematic sampling (SYS), with two sample sizes ($n = 9$ and $n = 16$). The green circles represent clusters of individuals. For systematic sampling, with $n = 9$ (2nd column), the cluster diameter is inferior to the inter-unit distance, so some clusters can be missed, but there is never more than one unit in each cluster. With $n = 16$ (4th column), the cluster diameter equals the inter-unit distance; all clusters present in the study area are sampled at least once in every sample. This leads to a lower sampling variance for systematic sampling than random sampling, in which the proportion of units located in clusters varies more between samples (1st and 3rd columns).

pulations, and the variance ratio reached similar values than for the virtual populations. Thus, sampling methods with a balanced spatial coverage seem to yield more precise estimates than SRS, even for populations with more complex spatial structures than our virtual populations. However, two differences emerged : (1) the variance ratio did not exhibit a localised minimum at the point where the mean distance between sampling units equalled the diameter of the clusters and instead appeared to be stable for sample sizes above $n = 200$; and (2) SYS and SBS seemed to have roughly similar precision. We expected that the variance ratio curves would not have a minimum as clearly localised for natural populations as for virtual populations. Indeed, for populations consisting of clusters with various sizes and densities of individuals, it is likely that multiple sample sizes may yield a similar proportion of units located in the clusters and, therefore, a similar relative precision. The fact that SYS and SBS achieved a similar precision could stem from the same phenomenon, but this requires further investigation.

Further studies need to be conducted to identify the other characteristics of the distribution of individuals than the diameter of the clusters involved for natural populations. This will first require to better understand how individuals are distributed within natural populations. Currently, datasets containing the location of all individuals in a population, or more synthetic aggregation metrics, remain scarce (but see LAW et al., 2009 ; MORRISON et al., 2008), making it difficult to build simulations with realistic distributions of individuals. Once this barrier is removed, simulation studies will have to be carried out to identify the characteristics other than cluster diameter that drive the relative precision of sampling methods. For example, the non-random location of clusters, heterogeneity in cluster size and shape, or heterogeneity in density between clusters and within each cluster might be good candidates. Finally, metrics that can be measured easily in the field will have to be identified so that the sampling design can be adapted to the spatial structure of the population. This last step will be critical for the results of future methodological work to be implemented in the field.

2.4.3 Recommendations for field studies

Given our results on both virtual and natural populations, we recommend using SYS or SBS when studying populations with signs of spatial aggregation. These sampling methods will, on average, provide more precise estimates than SRS unless the

clusters are of similar size to the sampling units, in which case all sampling methods will achieve equivalent precision. However, as the results between simulations and natural populations differed, we do not recommend SYS over SBS, as both methods might provide roughly equivalent precision estimates for natural populations.

To check whether it is worthwhile to choose SYS or SBS instead of SRS, cluster diameter measurements can be used to verify if the planned sample size allows a large increase in precision or not. If clusters are identifiable in the study area, one can randomly select clusters and measure their greatest width. If the median diameter is close to the mean inter-unit distance obtained for the planned sample size, the increase in precision will be large. For the plant populations we mapped, the median cluster diameter we measured identified sample sizes for which SYS and SBS were much more precise than SRS. Another solution proposed by KERMORVANT et al. (2020) is to use the available information on the population (i.e. results from a pilot study, expert knowledge, etc.) to simulate a virtual population with a distribution of individuals as close as possible to the studied population, and to perform sampling simulations to identify the optimal sampling design. Furthermore, the consequence of the better spatial coverage of SYS and SBS compared to SRS is that the distance to visit all sample units is generally greater. If travel time is a strong constraint and the expected gain in precision is low, SRS might be favoured over the other methods.

Field ecologists should be aware that SYS has a statistical drawback. For SYS, the sample mean is an unbiased estimator of the population mean, but there is no universally unbiased estimator for the variance of this estimate, i.e. the sampling variance (COCHRAN, 1977, p.224). In other words, all existing estimators can sometimes give biased estimates of the sampling variance so that although the population mean will be estimated without bias, the precision of this estimate can be under- or overestimated (MAGNUSSEN & FEHRMANN, 2019). Nevertheless, we argue that this problem should not prevent using SYS, given the substantial potential increase in precision using this sampling method. The search for better estimators is an ongoing research topic, and the best estimators currently known usually allow to see a substantial gain in precision by shifting from SRS to SYS, although variances tend to be slightly overestimated. For example, the two best estimators found by MCGARVEY et al. (2016) overestimated the

sampling variance by less than 20% for most populations, although cases of overestimation above 60% were found for a few populations. Simulating even more populations, MAGNUSSEN et al. (2020) found two other estimators to overestimate sampling variance on average by less than 10%. We tested these four estimators on our virtual and natural populations (Appendix 4). For the virtual populations, the four estimators overestimated the sampling variance, which was expected given that they are all based on measurements of the correlation among neighbouring units. This is not adapted for populations following a Matérn cluster process as in our simulations. However, we propose a new estimator that is more adapted for this type of populations, and it provided nearly unbiased estimates of the sampling variance. For the natural populations, we found similar levels of performance to previous studies (MAGNUSSEN et al., 2020; MCGARVEY et al., 2016), with several estimators based on correlation between neighbouring units, as well as our new estimator, providing almost unbiased estimates of the sampling variance. Estimating sampling variance is less problematic for SBS, although some cases of biased estimates have also been reported (ROBERTSON et al., 2013; STEVENS & OLSEN, 2004). We tested the most commonly used estimator, and it provided nearly unbiased estimates for both the virtual and natural populations (Appendix 4). These results confirm that given a variance estimator appropriate for the studied population is used, a substantial gain in precision will be seen when using SYS or SBS instead of SRS. To help choose the variance estimator, future simulation studies need to be conducted to screen the performance of estimators across many distributions of individuals. This will be particularly useful if realistic distributions of individuals can be simulated based on a better understanding of how individuals are distributed in natural populations. Other advantages of SBS over the other two methods include the ability to incorporate legacy sites where data have already been accumulated (FOSTER et al., 2017) and to draw oversamples to replace units that could not be observed in the field (e.g. inaccessible sites) while maintaining spatially balanced samples (KERMORVANT et al., 2019).

The results of this paper refer to design-based inference, in which the estimates of the population mean and sampling variance are generally unbiased (except for SYS as discussed above), and no assumptions about the studied population need to be made. Model-based inference is an alternative approach in which the estimates are obtained

by fitting a spatial variation model to the sample. This approach usually provides more precise estimates than design-based inference when there is spatial dependence in the density of individuals. Yet, the accuracy of this approach strongly relies on the realism of model assumptions, and unrealistic assumptions can lead to spurious estimates. Moreover, hybrid methods, called model-assisted inference, which combine the advantages of both approaches have been developed (BRUS, 2021). Using model-based or preferably model-assisted inference seems a promising way to further increase the precision of estimates for aggregated populations. However, the difference in estimate precision between design-based and model-based approaches seems limited when the sample is selected with a spatially balanced sampling method, while it is large with SRS (DUMELLE et al., 2022). Finding ways to combine the strengths of model-assisted inference and spatially balanced sampling methods tailored to the aggregation of the studied population would be the next step to further improve the precision of aggregated population size estimates.

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Data availability

All data and R codes used for this study are available from the GitHub repository : https://github.com/JanPerret/Sampling_aggregated_populations. The repository is also archived on Zenodo (Perret, 2022).

Authors' contributions

Jan Perret, Anne Charpentier, Guillaume Papuga and Aurélien Besnard conceived the study and designed the methodology; Jan Perret and Roger Pradel analysed the data; Jan Perret led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest statement

All authors declare no conflicts of interest.

References

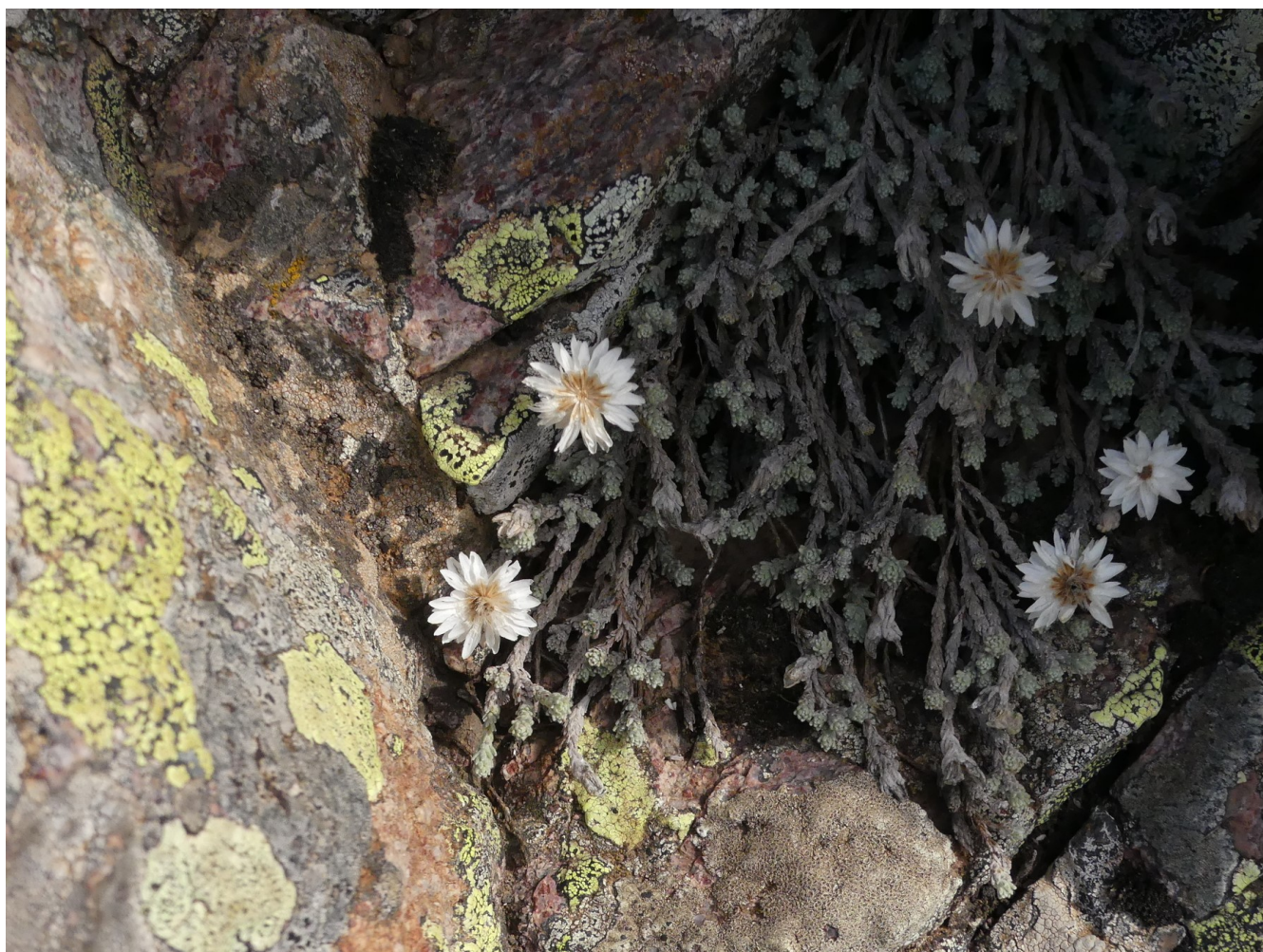
- AMBROSIO, L., IGLESIAS, L., MARÍN, C., & DEL MONTE, J. P. (2004). Evaluation of sampling methods and assessment of the sample size to estimate the weed seedbank in soil, taking into account spatial variability. *Weed Research*, 44(3), 224-236. <https://doi.org/10.1111/j.1365-3180.2004.00394.x> (cf. p. 111)
- BADDELEY, A., RUBAK, E., & TURNER, R. (2015). *Spatial Point Patterns : Methodology and Applications with R*. Chapman ; Hall/CRC Press. <https://doi.org/10.1201/b19708>. (Cf. p. 99, 100, 105)
- BEISSINGER, S. R., & MCCULLOUGH, D. R. (2002). *Population Viability Analysis*. University of Chicago Press. (Cf. p. 95).
- BJØRNSTAD, O. N., & GRENFELL, B. T. (2001). Noisy clockwork : time series analysis of population fluctuations in animals. *Science*, 293(5530), 638-643. <https://doi.org/10.1126/science.1062226> (cf. p. 95)
- BRUS, D. J. (2021). Statistical approaches for spatial sample survey : Persistent misconceptions and new developments. *European Journal of Soil Science*, 72(2), 686-703. <https://doi.org/10.1111/ejss.12988> (cf. p. 103, 117)
- COCHRAN, W. G. (1946). Relative Accuracy of Systematic and Stratified Random Samples for a Certain Class of Populations. *The Annals of Mathematical Statistics*, 17(2), 164-177. <https://doi.org/10.1214/aoms/1177730978> (cf. p. 97)
- COCHRAN, W. G. (1977). *Sampling Techniques* (3rd). John Wiley & Sons. (Cf. p. 95-98, 101, 111, 112, 115).
- CROW, J. F. (2010). Wright and Fisher on Inbreeding and Random Drift. *Genetics*, 184(3), 609-611. <https://doi.org/10.1534/genetics.109.110023> (cf. p. 95)
- DAMGAARD, C. F., & IRVINE, K. M. (2019). Using the beta distribution to analyse plant cover data. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13200> (cf. p. 96)
- DANCHIN, E., & WAGNER, R. H. (1997). The evolution of coloniality : the emergence of new perspectives. *Trends in Ecology & Evolution*, 12(9), 342-347. [https://doi.org/10.1016/S0169-5347\(97\)01124-5](https://doi.org/10.1016/S0169-5347(97)01124-5) (cf. p. 96)

- DENNIS, B., MUNHOLLAND, P. L., & SCOTT, J. M. (1991). Estimation of Growth and Extinction Parameters for Endangered Species. *Ecological Monographs*, 61(2), 115-143. <https://doi.org/10.2307/1943004> (cf. p. 95)
- DUMELLE, M., HIGHAM, M., VER HOEF, J. M., OLSEN, A. R., & MADSEN, L. (2022). A comparison of design-based and model-based approaches for finite population spatial sampling and inference. *Methods in Ecology and Evolution*, 13(9), 2018-2029. <https://doi.org/10.1111/2041-210X.13919> (cf. p. 117)
- FOSTER, S. D., HOSACK, G. R., LAWRENCE, E., PRZESLAWSKI, R., HEDGE, P., CALEY, M. J., BARRETT, N. S., WILLIAMS, A., LI, J., LYNCH, T., DAMBACHER, J. M., SWEATMAN, H. P. A., & HAYES, K. R. (2017). Spatially balanced designs that incorporate legacy sites. *Methods in Ecology and Evolution*, 8(11), 1433-1442. <https://doi.org/10.1111/2041-210X.12782> (cf. p. 116)
- FRANKHAM, R. (1995). Effective population size/adult population size ratios in wildlife : a review. *Genetics Research*, 66(2), 95-107. <https://doi.org/10.1017/S0016672300034455> (cf. p. 95)
- GREIG-SMITH, P. (1983). *Quantitative Plant Ecology*. University of California Press. (Cf. p. 96, 100).
- HINDE, A. (1956). The Biological Significance of the Territories of Birds. *Ibis*, 98(3), 340-369. <https://doi.org/10.1111/j.1474-919X.1956.tb01419.x> (cf. p. 96)
- IUCN. (2019). Guidelines for Using the IUCN Red List Categories and Criteria - Version 14. (Cf. p. 95).
- KERMORVANT, C., COUBE, S., D'AMICO, F., BRU, N., & CAILL-MILLY, N. (2020). Sequential process to choose efficient sampling design based on partial prior information data and simulations. *Spatial Statistics*, 38, 100439. <https://doi.org/10.1016/j.spasta.2020.100439> (cf. p. 98, 115)
- KERMORVANT, C., D'AMICO, F., BRU, N., CAILL-MILLY, N., & ROBERTSON, B. (2019). Spatially balanced sampling designs for environmental surveys. *Environmental Monitoring and Assessment*, 191(8), 524. <https://doi.org/10.1007/s10661-019-7666-y> (cf. p. 111, 112, 116)
- KHAEMBA, W. M., STEIN, A., RASCH, D., DE LEEUW, J., & GEORGIADIS, N. (2001). Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. *African Journal of Ecology*, 39(4), 374-382. <https://doi.org/10.1046/j.0141-6707.2001.00329.x> (cf. p. 98)
- KISH, L. (1965). *Survey Sampling*. John Wiley & Sons. (Cf. p. 104).
- LARA-ROMERO, C., CRUZ, M. d. I., ESCRIBANO-ÁVILA, G., GARCÍA-FERNÁNDEZ, A., & IRIONDO, J. M. (2016). What causes conspecific plant aggregation? Disentangling the role of dispersal, habitat heterogeneity and plant-plant interactions. *Oikos*, 125(9), 1304-1313. <https://doi.org/https://doi.org/10.1111/oik.03099> (cf. p. 96)
- LAW, R., ILLIAN, J., BURSLEM, D. F. R. P., GRATZER, G., GUNATILLEKE, C. V. S., & GUNATILLEKE, I. a. U. N. (2009). Ecological information from spatial patterns of plants : insights from point process theory. *Journal of Ecology*, 97(4), 616-628. <https://doi.org/10.1111/j.1365-2745.2009.01510.x> (cf. p. 114)
- LEGENDRE, P. (1993). Spatial Autocorrelation : Trouble or New Paradigm? *Ecology*, 74(6), 1659-1673. <https://doi.org/10.2307/1939924> (cf. p. 96)
- LEVIN, S. A. (1992). The Problem of Pattern and Scale in Ecology. *Ecology*, 73(6), 1943-1967. <https://doi.org/10.2307/1941447> (cf. p. 96)
- MAGNUSSEN, S., & FEHRMANN, L. (2019). In search of a variance estimator for systematic sampling. *Scandinavian Journal of Forest Research*, 34(4), 300-312.

- <https://doi.org/10.1080/02827581.2019.1599063> (cf. p. 103, 115)
- MAGNUSSEN, S., MCROBERTS, R. E., BREIDENBACH, J., NORD-LARSEN, T., STÄHL, G., FEHRMANN, L., & SCHNELL, S. (2020). Comparison of estimators of variance for forest inventories with systematic sampling - results from artificial populations. *Forest Ecosystems*, 7(1), 17. <https://doi.org/10.1186/s40663-020-00223-6> (cf. p. 103, 104, 116)
- MAHER, C. R., & LOTT, D. F. (2000). A Review of Ecological Determinants of Territoriality within Vertebrate Species. *The American Midland Naturalist*, 143(1), 1-29. [https://doi.org/10.1674/0003-0031\(2000\)143\[0001:AROEDO\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2000)143[0001:AROEDO]2.0.CO;2) (cf. p. 96)
- MATÉRN, B. (1986). *Spatial Variation* (2nd). Springer. <https://doi.org/10.1007/978-1-4615-7892-5>. (Cf. p. 97, 100, 109)
- MCDONALD, T., & MCDONALD, A. (2020). SDraw : Spatially Balanced Samples of Spatial Objects. (Cf. p. 105).
- MCGARVEY, R., BURCH, P., & MATTHEWS, J. M. (2016). Precision of systematic and random sampling in clustered populations : habitat patches and aggregating organisms. *Ecological Applications*, 26(1), 233-248. <https://doi.org/10.1890/14-1973> (cf. p. 96-98, 103, 109, 111, 115, 116)
- MIER, K. L., & PICQUELLE, S. J. (2008). Estimating abundance of spatially aggregated populations : Comparing adaptive sampling with survey designs. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(2), 176-197. <https://doi.org/10.1139/F07-138> (cf. p. 98, 111)
- MORALES, Y., WEBER, L. J., MYNETT, A. E., & NEWTON, T. J. (2006). Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. *Journal of the North American Benthological Society*, 25(3), 664-676. [https://doi.org/10.1899/0887-3593\(2006\)25\[664:EOSAHC\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2006)25[664:EOSAHC]2.0.CO;2) (cf. p. 96)
- MORRISON, L. W., SMITH, D., YOUNG, C., & NICHOLS, D. (2008). Evaluating sampling designs by computer simulation : A case study with the Missouri bladderpod. *Population Ecology*, 50(4), 9. <https://doi.org/10.1007/s10144-008-0100-x> (cf. p. 96, 98, 100, 111, 114)
- PHILIPPI, T. (2005). Adaptive Cluster Sampling for Estimation of Abundances Within Local Populations of Low-Abundance Plants. *Ecology*, 86(5), 1091-1100. <https://doi.org/10.1890/04-0621> (cf. p. 96)
- QUENOUILLE, M. H. (1949). Problems in Plane Sampling. *The Annals of Mathematical Statistics*, 20(3), 355-375. <https://doi.org/10.1214/AOMS/1177729989> (cf. p. 97, 109)
- QUÉROUÉ, M., BARBRAUD, C., BARRAQUAND, F., TUREK, D., DELORD, K., PACOUREAU, N., & GIMENEZ, O. (2021). Multispecies integrated population model reveals bottom-up dynamics in a seabird predator-prey system. *Ecological Monographs*, 91(3), e01459. <https://doi.org/10.1002/ecm.1459> (cf. p. 95)
- R CORE TEAM. (2019). R : A Language and Environment for Statistical Computing. (Cf. p. 105).
- RAYBURN, A. P., & SCHUPP, E. W. (2013). Effects of community- and neighborhood-scale spatial patterns on semi-arid perennial grassland community dynamics. *Oecologia*, 172(4), 1137-1145. <https://doi.org/10.1007/s00442-012-2567-6> (cf. p. 96)
- REISCH, C., SCHMID, C., & HARTIG, F. (2018). A comparison of methods for estimating plant population size. *Biodiversity and Conservation*, 27(8), 2021-2028. <https://doi.org/10.1007/s10531-018-1522-1> (cf. p. 100)

- RIPPLE, W. J., & BESCHTA, R. L. (2012). Trophic cascades in Yellowstone : The first 15 years after wolf reintroduction. *Biological Conservation*, 145(1), 205-213. <https://doi.org/10.1016/j.biocon.2011.11.005> (cf. p. 95)
- ROBERTSON, B., BROWN, J. A., MCDONALD, T., & JAKSONS, P. (2013). BAS : Balanced Acceptance Sampling of Natural Resources. *Biometrics*, 69(3), 776-784. <https://doi.org/10.1111/biom.12059> (cf. p. 97, 101, 112, 116)
- ROBERTSON, B., MCDONALD, T., PRICE, C., & BROWN, J. (2018). Halton iterative partitioning : spatially balanced sampling via partitioning. *Environmental and Ecological Statistics*, 25(3), 305-323. <https://doi.org/10.1007/s10651-018-0406-6> (cf. p. 101)
- ROBINSON, P. (1954). The Distribution of Plant Populations. *Annals of Botany*, 18(69), 35-45. <https://doi.org/10.1093/oxfordjournals.aob.a083380> (cf. p. 96)
- SEABLOOM, E. W., BJORNSTAD, O. N., BOLKER, B. M., & REICHMAN, O. J. (2005). Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecological Monographs*, 75(2), 199-214. <https://doi.org/10.1890/03-0841> (cf. p. 96)
- SHACKLETON, R. T., PETITPIERRE, B., PAJKOVIC, M., DESSIMOZ, F., BRÖNNIMANN, O., CATTIN, L., ČEJKOVÁ, Š., KULL, C. A., PERGL, J., PYŠEK, P., YOCCOZ, N., & GUIBAN, A. (2020). Integrated Methods for Monitoring the Invasive Potential and Management of *Heracleum mantegazzianum* (giant hogweed) in Switzerland. *Environmental Management*, 65(6), 829-842. <https://doi.org/10.1007/s00267-020-01282-9> (cf. p. 97)
- SIMBERLOFF, D., MARTIN, J.-L., GENOVESI, P., MARIS, V., WARDLE, D. A., ARONSON, J., COURCHAMP, F., GALIL, B., GARCIA-BERTHOUS, E., PASCAL, M., PYSEK, P., SOUSA, R., TABACCHI, E., & VILA, M. (2013). Impacts of biological invasions : what's what and the way forward. *Trends in Ecology & Evolution*, 28(1), 58-66. <https://doi.org/10.1016/j.tree.2012.07.013> (cf. p. 95)
- SMITH, A., ANDERSON, M. J., & PAWLEY, M. D. M. (2017). Could ecologists be more random? Straightforward alternatives to haphazard spatial sampling. *Ecography*, 40(11), 1251-1255. <https://doi.org/10.1111/ecog.02821> (cf. p. 97)
- SMITH, D., ROGALA, J. T., GRAY, B. R., ZIGLER, S. J., & NEWTON, T. J. (2011). Evaluation of Single and Two-Stage Adaptive Sampling Designs for Estimation of Density and Abundance of Freshwater Mussels in a Large River. *River Research and Applications*, 27(1), 122-133. <https://doi.org/10.1002/rra.1334> (cf. p. 96, 98)
- STEVENS, D. L., & OLSEN, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association*, 99(465), 262-278. <https://doi.org/10.1198/016214504000000250> (cf. p. 97, 112, 116)
- STOLL, P., & BERGIUS, E. (2005). Pattern and process : competition causes regular spacing of individuals within plant populations. *Journal of Ecology*, 93(2), 395-403. <https://doi.org/10.1111/j.0022-0477.2005.00989.x> (cf. p. 96)
- THOMPSON, S. (1990). Adaptive Cluster Sampling. *Journal of the American Statistical Association*, 85(412), 1050-1059. <https://doi.org/10.2307/2289601> (cf. p. 96)
- THOMPSON, S. (2012). *Sampling* (3rd). Wiley. (Cf. p. 95, 103).
- THOMPSON, W. (2004). *Sampling Rare or Elusive Species : Concepts, Designs, and Techniques for Estimating Population Parameters* (2nd). Island Press. (Cf. p. 96).

- TURK, P., & BORKOWSKI, J. J. (2005). A review of adaptive cluster sampling : 1990–2003. *Environmental and Ecological Statistics*, 12(1), 55-94. <https://doi.org/10.1007/s10651-005-6818-0> (cf. p. 96)
- WATSON, J., & ESTES, J. A. (2011). Stability, resilience, and phase shifts in rocky sub-tidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs*, 81(2), 215-239. <https://doi.org/10.1890/10-0262.1> (cf. p. 95)
- YOCCOZ, N. G., NICHOLS, J. D., & BOULINIER, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16(8), 446-453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4) (cf. p. 96)



Immortelle des frimas (*Castroviejoa frigida*), Monte Cinto, Corse, septembre 2020.

Chapitre 3

Les plantes sont immobiles mais se cachent :
la détection imparfaite et hétérogène est la
règle lors du comptage de plantes

Dans le deuxième chapitre, nous avons vu comment améliorer la précision des estimations de taille de population en adaptant le plan d'échantillonnage à l'agrégation des individus. Comme l'étude portait sur l'échantillonnage, elle a été réalisée en considérant qu'il n'y avait aucune erreur d'observation. Cependant, comme nous l'avons vu dans le premier chapitre, les erreurs d'observation, et en particulier la détection imparfaite, sont un problème très fréquent des suivis de population, qui est peu étudié pour les plantes. L'objectif de ce troisième chapitre était de vérifier formellement que la détection des individus est imparfaite lors de comptages de plantes non marquées, une métrique couramment utilisée pour suivre les populations de plantes. Pour cela, j'ai réalisé une expérience au cours de laquelle des observateurs ont compté des individus dans des quadrats de 1 x 1 m, et ce pour 30 espèces et dans différents habitats. Les résultats ont montré que la détection des individus était effectivement imparfaite, et ont permis de décrire l'effet des principales variables écologiques et observationnelles sur la probabilité de détection des individus. L'approche expérimentale a permis d'obtenir des estimations plus précises des effets des multiples variables étudiées et de leurs interactions, et de s'assurer que les résultats n'étaient pas influencés par des facteurs confondants majeurs, ce qui aurait été difficile à obtenir avec une étude observationnelle basée sur un jeu de données existant.

L'article correspondant à ce chapitre a été soumis à la revue *Journal of Ecology* le 22 septembre 2022 et j'ai renvoyé l'article suite à une révision majeure le 21 décembre 2022. J'ai présenté les résultats préliminaires de cette étude via une présentation orale aux rencontres des acteurs de la conservation de la flore méditerranéenne (RESEDA Flore) à Aix-en-Provence le 6 décembre 2021, puis les résultats finaux à l'*International conference in Ecology and Evolution* (SFE2, GfÖ, EEF) à Metz le 23 novembre 2022.

Plants stand still but hide : imperfect and heterogeneous detection is the rule when counting plants

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Abstract

1. The estimation of population size and its variation across space and time largely relies on counts of individuals, generally carried out within spatial units such as quadrats or sites. Missing individuals during counting (i.e. imperfect detection) results in biased estimates of population size and trends. Imperfect detection has been shown to be the rule in animal studies, and most studies now correct for this bias by estimating detection probability. Yet this correction remains exceptional in plant studies, suggesting that most plant ecologists implicitly assume that all individuals are always detected.
2. To assess if this assumption is valid, we conducted a field experiment to estimate individual detection probability in plant counts conducted in 1x1 m quadrats. We selected 30 herbaceous plant species along a gradient of conspicuousness at 24 sites along a gradient of habitat closure, and asked groups of observers to count individuals in 10 quadrats using three counting methods requiring progressively increasing times to complete (quick count, unlimited count and cell count). In total, 158 participants took part in the experiment, allowing an analysis of the results of 5,024 counts.
3. Over all field sessions, no observer succeeded in detecting all the individuals in the 10 quadrats. The mean detection rate was 0.44 (ranging from 0.11 to 0.82) for the quick count, 0.59 for the unlimited count (range 0.18–0.87) and 0.74 for the cell count (range 0.46–0.94).
4. Detection probability increased with the conspicuousness of the target species and decreased with the density of individuals and habitat closure. The observer's experience in botany had little effect on detection probability, whereas detection was strongly affected by the time observers spent counting. Yet although the more time-consuming methods increased detection probability, none achieved perfect detection, nor did they reduce the effect on detection probability of the variables we measured.
5. *Synthesis.* Our results show that detection is imperfect and highly heterogeneous when counting plants. To avoid biased estimates when assessing the size, temporal or spatial trends of plant populations, plant ecologists should use methods

that estimate the detection probability of individuals rather than relying on raw counts.

Keywords— conservation - demography - detectability - field methods - N-mixture - observer effect - plant survey - population monitoring

3.1 Introduction

Population size and the variability of population size over time and space are of central importance in ecology and conservation. These parameters are required to understand ecosystem dynamics (RIPPLE & BESCHTA, 2012; WATSON & ESTES, 2011), assess population viability (DENNIS et al., 1991) and trigger conservation policies and actions (e.g. IUCN, 2019). Population size estimates largely rely on counts of individuals, generally made in spatial units such as quadrats or sites (ELPHICK, 2008; YOCCOZ et al., 2001). Therefore, the accuracy of these counts is crucial, as counting errors would result in biased estimates of population sizes and trends.

When carrying out counts, observers can miss some individuals, in effect counting fewer individuals than were present in the sampling units. This phenomenon of imperfect detection, well known in animal studies, leads to underestimating population sizes (WILLIAMS et al., 2002). If detection is imperfect but constant over time and space, raw counts can provide unbiased estimates of population trends or spatial variation (YOCCOZ et al., 2001). However, if detection varies over time (e.g. across the sampling season or between years) or space (e.g. between habitats), the raw differences between counts performed at different sampling sessions or in different sampling units are a mixture of differences in abundance and detection (KÉRY et al., 2009). For example, a decrease in population size over the years may be hidden as observers improve their ability to detect individuals over time (KENDALL et al., 1996). Or one might conclude that there are fewer individuals in closed than in open habitats because they are harder to detect in closed habitats (BUCKLAND et al., 2008). Even differences as small as 4–8% in detection dramatically increase the risk of erroneously concluding that population size varies over time or space (ARCHAUX et al., 2012).

Since the 1970s, many studies on vertebrates have shown that imperfect detection

is the rule and that detection probability tends to vary in time and space. Detection probability depends on a number of factors : the observation process (both the observation method and the survey effort), the visibility of the target species, and the characteristics of its habitat (KÉRY et al., 2005; KÉRY & SCHMIDT, 2008; PETITOT et al., 2014). Consequently, studies including an estimate of detection probability, which corrects for the bias resulting from imperfect detection, have become increasingly common for vertebrates and, to a lesser extent, invertebrates. Yet, they remain exceptional for plants (KELLNER & SWIHART, 2014), suggesting that most plant ecologists implicitly assume that all individuals are always detected or that differences in detection probability are negligible. It is true that, unlike most animals, plants are immobile, and observers may thus consider it unlikely to miss individuals if careful sampling is conducted. This assumption led John Harper to make the famous statement 'Plants stand still and wait to be counted', comparing the ease of studying plant and animal populations (HARPER, 1977).

Although detection has almost never been investigated in plants at the individual level, some studies have investigated it at the species level, assessing species occurrence in a given area using two main approaches : occupancy or time-to-detection designs. In the first approach, the survey duration is fixed, and the detection probability of the species when surveying quadrats or sites is estimated from repeated surveys. In the second approach, the detection probability is estimated based on the survey time required to detect the species. These studies found that the detection of plant species was almost always imperfect and that detection probability varied depending on ecological and observational variables. For example, species detection varied according to the morphology of the target species (CHEN et al., 2013; CHEN et al., 2009; GARRARD et al., 2013), with conspicuous growth forms and phenological stages raising detection probability. A high density of individuals increased the probability of detecting the species (BORNAND et al., 2014), while the closure of the surrounding habitat decreased it (ALEXANDER et al., 2012; GARRARD et al., 2008). Species detection probability also increased with survey effort (CHEN et al., 2009) and often varied between observers (ARCHAUX et al., 2006; GARRARD et al., 2008). Although these studies confirm that detection issues exist when assessing the occurrence of plant species, do these issues affect individual detection to a similar extent ?

Concerning detection at the individual level, the only studies that have been conducted on plants used marked individuals in so-called ‘capture–recapture’ designs (LEBRETON et al., 1992) or the time-to-detection of individuals (HAUSER et al., 2022). These studies found that individual detection was imperfect, although individuals were generally searched for in relatively small, intensively surveyed plots (ALEXANDER et al., 1997; ANDRIEU et al., 2017; KÉRY & GREGG, 2003). In most studies using marked individuals, individual detection probability varied with the phenological stage of individuals and sometimes with habitat closure (ANDRIEU et al., 2017; MOORE et al., 2011). HAUSER et al. (2022) showed that flowering individuals were detected faster than non-flowering ones, and that the abundance of individuals of species resembling the target species delayed detection. Observers with recent experience in searching for the target species detected it faster, confirming at the individual level what has been demonstrated at the species level. Therefore, it is of particular concern that individual detection probability has never been estimated for counts of unmarked plants, despite this being one of the most commonly used methods for estimating population sizes and trends in plant ecology (ELZINGA & SALZER, 1998; REISCH et al., 2018). In addition, many studies in plant ecology estimate vital rates by counting unmarked individuals per life stage (e.g. GILJOHANN et al., 2017; MOLANO-FLORES & BELL, 2012). In theory, data from capture-recapture designs could be used to estimate detection probability and correct estimates from counts of unmarked individuals. To our knowledge, this has never been done, probably because it would be very impractical since both observation processes would have to be strictly equivalent regarding detection and because estimating detection probability directly from counts of unmarked plants is usually less labour–intensive (ROYLE, 2004).

To assess whether imperfect detection of individuals is indeed the rule in plant counts, we conducted a field experiment in which observers counted plants in 1x1 m quadrats, a commonly used quadrat size (ELZINGA & SALZER, 1998; GAUTHIER et al., 2019; GAUTHIER et al., 2017). The experiment covered 30 species and 300 quadrats, and involved 158 observers who made 5,024 counts. Our study had three aims : (i) to estimate the detection probability of individuals in plant counts ; (ii) to estimate how detection probability varies in time and space ; (iii) to determine if increasing the survey effort results in a higher detection probability, and could allow reaching perfect

detection. To meet these objectives, we tested whether detection varies according to ecological variables (species conspicuousness, true population density and surrounding habitat closure) and observational variables (counting method and experience of observers), which are likely to vary over time and space, as well as testing varying degrees of survey effort.

3.2 Materials and methods

3.2.1 Selection of sites, species and observers

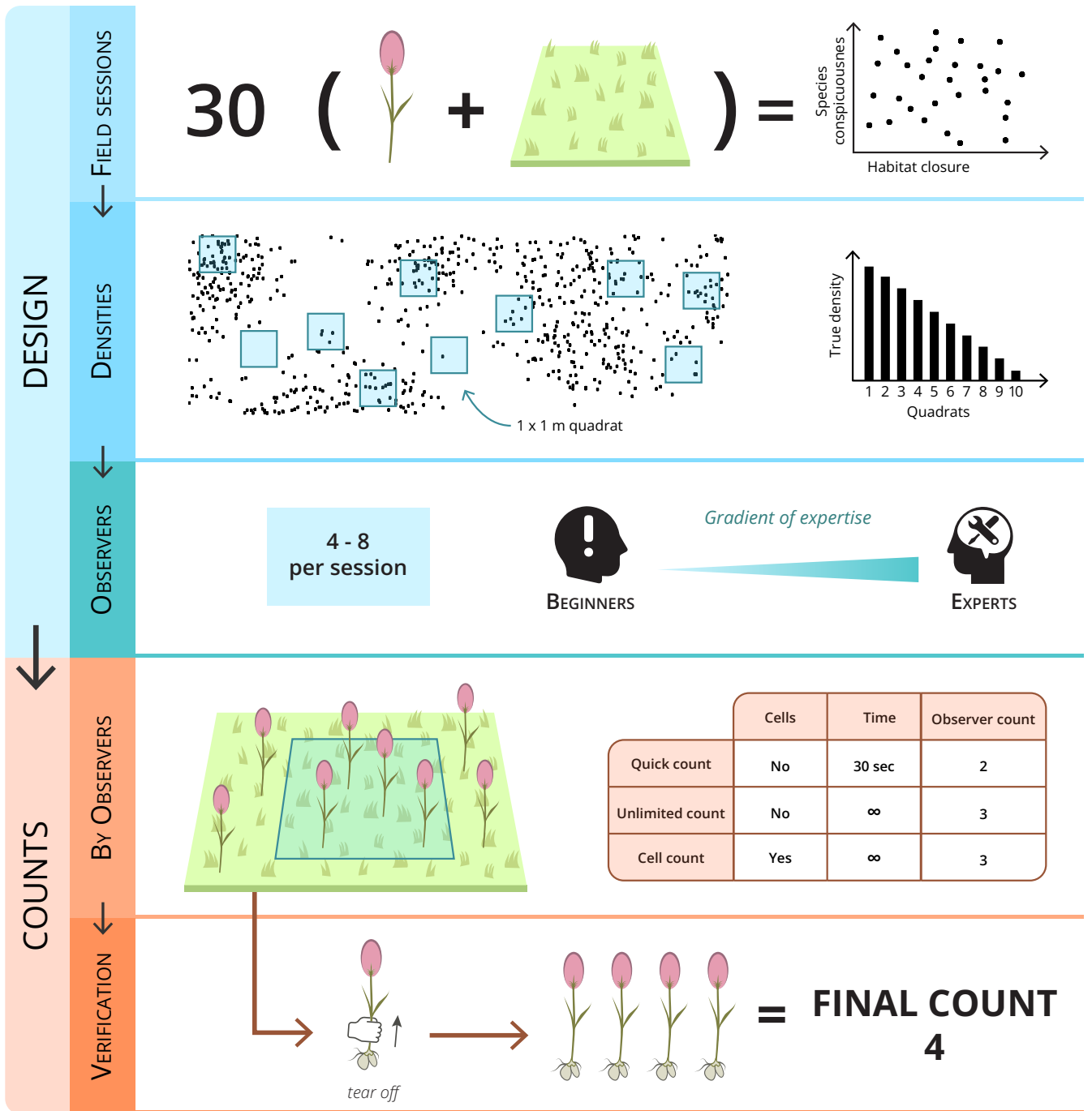
We selected 30 herbaceous plant species from 24 sites throughout France in Mediterranean, Alpine and temperate climatic regions (Appendix 1). We chose species with various growth forms and phenological stages to cover a gradient from cryptic to conspicuous species. As the experiment focused on counting individuals, we selected only species for which ‘individuals’ (ramets or genets depending on the species) could be unambiguously differentiated. We avoided species difficult to identify so that all could be identified at first glance without having to check identification criteria on each detected individual. We selected study sites to cover a gradient of habitat closure, from bare ground to dense meadows, to include all possible combinations of species conspicuousness and habitat closure (Fig. 3.1).

Participants were volunteers selected among our colleagues, researchers, undergraduate students and professionals involved in flora conservation. We selected 4 to 8 observers for each field session, including at least one with several years of field experience in botany, one with no experience in botany, and intermediate profiles. Observers were allowed to participate in up to three sessions, but these sessions had to be several weeks apart. This resulted in 171 participations by 158 unique observers. We conducted the fieldwork from 7 October 2020 to 6 August 2021.

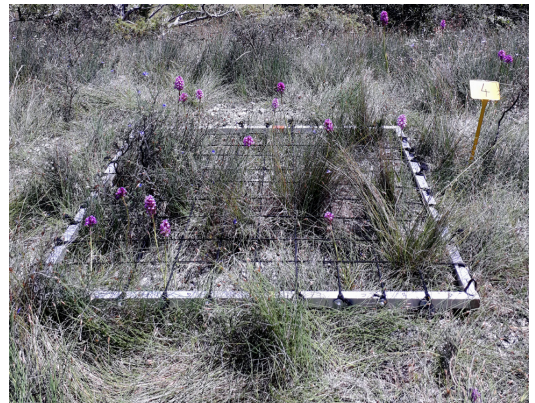
3.2.2 Experiment

Field setup and observer training

The fieldwork consisted of one-day sessions, during which a group of observers counted the number of individuals of a single target species in a habitat at one of the 24 sites.



A



B

FIGURE 3.1 – Diagram of the study’s experimental design. We conducted 30 field sessions, each focusing on a different species in a habitat with a different closure level, to cover the widest possible range of combinations of species conspicuousness and habitat closure. For each field session, we placed ten quadrats on the population to form a density gradient and chose 4–8 observers to have a gradient of experience in botany. The observers carried out three counting methods successively (quick, unlimited and cell counts). We then counted the true number of individuals by systematically digging out the individuals detected by the observers and then conducting an additional survey for any individuals that remained unnoticed. Picture A shows the experiment in progress at a Mediterranean site and picture B shows a quadrat with the cells.

The availability of participants restricted us to organise the field sessions. Whenever we had enough observers available somewhere, we prospected the landscape nearby to find an appropriate site (i.e. easy to access and with a habitat corresponding to what we needed to complete the habitat closure gradient). Then we searched for a suitable species, meeting our general criteria and completing the species conspicuousness gradient. Before the observers’ arrival, we placed ten 1x1 m quadrats on the target species population. We chose quadrat locations to ensure that (i) two were free of individuals of the target species (so that observers would not always expect to find individuals in the quadrats), and (ii) they covered a relatively linear gradient of densities up to a maximum of 150 individuals (when possible). It happened regularly that quadrats meant to be empty contained a few individuals and those with the highest densities contained more than 150 individuals. We labelled the quadrats from 1 to 10 and fixed them to the ground. When the observers arrived, we explained how the counts would be conducted and how to identify the target species at all phenological stages and differentiate it from the other species present at the study site. We then trained them to count on additional quadrats to check that everyone had understood the instructions. This training phase lasted until all observers felt comfortable with species identification and the counting methods. The entire training process usually took about an hour.

Counting methods

Each observer had to count the number of individuals of the target plant in each quadrat using three different methods, requiring a progressively increasing amount of survey time. In the first round, participants had 30 seconds to estimate the number of individuals in each quadrat (the quick count). In the second round, they had to count the number of individuals without any time limit (the unlimited count). We then divided

the quadrats into 100 cells of 10x10 cm (Fig. 3.1B), and observers performed the third round, where they had to count the number of individuals in each cell without any time limit (the cell count). This last method forced observers to survey the quadrat homogeneously and has been regularly used in the plant survey literature (e.g. GAUTHIER et al., 2019; GAUTHIER et al., 2017). For the unlimited and cell counts, observers recorded the time they spent counting in each quadrat. To avoid memory effects, after each round we collected the sheets on which the observers recorded their measurements, and observers surveyed the quadrats in a different order, approaching it from a different side at each round. The observers conducted the three counts on the ten quadrats in 1.5 to 5 hours (on average 3.25 hours).

Exhaustive count and measurement of covariates

After the observers had left, we carried out a final count to determine the true number of individuals present in each quadrat. This was done by searching each 10x10 cm cell for the maximum number of individuals detected by the observers during the third round and collecting them. Once the maximum number of individuals detected by the observers in each cell had been removed, we searched again for any potentially undetected individuals. This final count took between 1 and 7 hours (3 hours on average), depending on habitat closure and the number of individuals of the target species in the quadrats. Despite our verification method, we might have missed a few individuals during the final count, but we will refer to this as the 'true number of individuals' for the sake of simplicity. We calculated the detection probability of individuals by dividing the number of individuals detected by the observers by the true number of individuals present in each quadrat.

We measured three variables to investigate their effect on detection probability : an index of species conspicuousness (measured for each field session), an index of habitat closure (measured for each quadrat), and the experience in botany of the observers. For simplicity's sake, we used synthetic indices to characterise species conspicuousness and habitat closure. This allowed us to limit the number of variables and interactions in the model (e.g. species conspicuousness combines the average size of individuals, the presence of vividly coloured flowers, and the interaction of these variables). All the variables and interactions that we investigated in the following analysis are presented in

Table 3.1, as well as the underlying hypotheses. The way we measured the variables is detailed in Appendix 2.

3.2.3 Statistical analysis

In total, 300 quadrats were surveyed during the experiment by on average 5.7 observers, resulting in 5,024 counts. We removed 34 quadrats from the analysis that contained no individuals of the target species, as these do not provide information on detection probability. We withdrew four additional quadrats that unexpectedly contained more than 300 individuals to avoid the leverage effect due to these density outliers (Appendix 3). Keeping these quadrats in the dataset would have led to a reduction in the slope of the density effect, which could result from a nonlinear relationship at high densities, but with only four quadrats, we could not reliably test this hypothesis. In some cases ($N = 140$, representing 2.8% of the counts), the observers recorded more individuals than were truly present (Appendix 4). We thus carried out the analyses on two datasets, one in which we removed these counts and one in which we set these counts to the true number of individuals. As there was no discernible difference in the results, we present the results of the former analysis in the main text and the latter in Appendix 7. After all filtering steps, 4,319 counts remained in the dataset from which we had removed the observations with excess detections. We also performed the analyses keeping only the experienced botanists to verify that our results were not driven by an excess of novice observers in our sample. Despite some minor differences, our overall results remained unchanged (Appendix 8).

We used a generalised linear mixed model (GLMMs) with a binomial distribution and a logit link function to analyse the association between detection probability and the variables we measured and some of their interactions. There could be dependence between detections due to individuals forming clusters. However, observers often detected some but not all individuals within clusters. Furthermore, the aggregation of individuals was not very strong at the quadrat scale. Hence, the dependence between detections is probably relatively small, and we consider the binomial model appropriate. We designed the experiment to disentangle the effects on detection probability of species conspicuousness, habitat closure and survey effort. We had precise hypotheses about the mechanisms explaining these effects (detailed in Table 3.1) that included interactions

between variables, and we collected a large dataset to test all our hypotheses. Therefore, we fitted a single model including all the variables and interactions corresponding to our hypotheses and used their statistical significance for inference. To take into account the repeated measurements at each quadrat, we included random intercepts for the observers, the field sessions and the quadrats (nested within the field session). As the majority of observers participated in only one field session, we did not add a random effect interaction between observers and field sessions. Furthermore, we did not add random effects on the slopes because we had no specific hypothesis that would justify it. We standardised all the variables prior to model fitting and assessed the model's goodness-of-fit using the package DHARMA (HARTIG, 2022). We computed the proportion of variance explained by the model and the proportion of variance explained by the model's fixed effects, using the theoretical variance method of NAKAGAWA et al. (2017). Analyses were performed in R version 3.6.1 (R CORE TEAM, 2019), using packages lme4 (BATES et al., 2022) to fit the model and ggeffects (LÜDECKE et al., 2022) to plot the predictions.

TABLE 3.1 – Ecological variables (species conspicuousness, habitat closure, true density), observational variables (counting method, experience in botany, quadrat order, counting time), and interactions between variables tested for their effect on the detection probability of individuals, with our hypothesis about the underlying mechanisms. The measurement method of all variables is detailed in Appendix 2.

Variable	Description	Measurement method	Hypothesis	Type	Observed values
Species conspicuousness	Conspicuousness of the species at the time of the field session	Expert judgement based on the mean height of individuals and the presence of colourful flowers	Tall and colourful species are easier to detect, which increases their detection probability	Ordinal	1, 2, 3, 4
Habitat closure	Closure of the vegetation in the quadrat	Composite variable created from the vegetation height and the proportion of the area covered by vegetation in the quadrats (Appendix 2)	Dense vegetation masks individuals, which lowers detection probability	Continuous	-1.86 – 3.54

Variable	Description	Measurement method	Hypothesis	Type	Observed values
True density	Number of individuals present in the quadrat	Number of individuals counted in the quadrat by the experimenter at the end of the experiment	High density requires greater concentration and makes it difficult to distinguish between individuals, reducing detection probability	Count	0–295
Counting method	Counting method used	Fixed by the experimental design, each observer successively used the three counting methods on the ten quadrats	Counting methods requiring more survey time yield higher detection probability	Categorical	Quick count, unlimited count, cell count
Experience in botany	General experience in botany of the observer (not specific to the target species)	Self-evaluated by the observers before the experiment using a standardised form	Observers with more experience in botany have higher detection probability	Ordinal	1, 2, 3, 4, 5
Quadrat order	Position of the quadrat in the round	Defined by the experimental design, the order in which the observers investigated the quadrats was fixed in advance and different for each observer and round.	Learning increases detection probability over time, or fatigue decreases it	Continuous	1, 2, 3, ..., 10
Counting time	Time spent counting by the observer	Each observer timed the duration of counting	Spending more time increases detection probability	Continuous	Quick count : 0.5 min, Unlimited count : 0–11 min, Cell count : 0–41.58 min

Variable	Description	Measurement method	Hypothesis	Type	Observed values
Species conspicuousness x Habitat closure			Detection probability is less affected by habitat closure for conspicuous species	Interaction term	
Species conspicuousness x Counting method			Detection probability obtained with counting methods requiring more survey effort is less affected by species conspicuousness	Interaction term	
Habitat closure x Counting method			Detection probability obtained with counting methods requiring more survey time is less affected by habitat closure	Interaction term	
Experience in botany x Counting method			The difference in detection probability between experts and beginners is larger for the quick count than for the other two methods	Interaction term	
True density x Counting method			Counting methods requiring more survey time make it easier to distinguish between individuals, which decreases the negative effect of true density	Interaction term	
Quadrat order x Counting method			The effect of fatigue or learning on detection probability is stronger for counting methods requiring more survey time	Interaction term	

Variable	Description	Measurement method	Hypothesis	Type	Observed values
Species conspicuousness x Counting time x Counting method		No coefficient is estimated for the quick count as the time was fixed	Spending an additional extra minute further increases detection probability for species that are easy to detect	Interaction term	
Habitat closure x Counting time x Counting method		No coefficient is estimated for the quick count as the time was fixed	Spending an additional extra minute further increases detection probability in sparse vegetation	Interaction term	

3.3 Results

Over the 30 field sessions, no observer succeeded in detecting all the individuals in all the quadrats. Averaged over all quadrats and observers, the mean detection rate per field session was 0.44 (ranging from 0.11 to 0.82) for the quick count, 0.59 for the unlimited count (from 0.18 to 0.87), and 0.74 for the cell count (from 0.46 to 0.94).

The goodness-of-fit of the fitted model was very good (Appendix 5). All ecological and observational variables were significantly correlated with detection probability in at least some conditions, i.e. for some counting methods or some levels of the other variables (Fig. 3.2; Appendix 6). Regarding the ecological variables, as expected, the more closed the habitat, the lower the detection probability (Fig. 3.3). The more conspicuous the species, the higher the detection probability, except in entirely open habitats, where the detection probability was constant and high regardless of the conspicuousness of the species (Fig. 3.3). Detection probability decreased steeply with the true density, in a similar way for the three counting methods (Fig. 3.4). Regarding the observational variables, spending more time sharply increased detection probability for the unlimited and cell counts. Habitat closure moderated this trend, i.e. spending an extra minute counting increased detection probability less in closed habitats than in open habitats. Experienced observers achieved slightly higher detection probability than inexperienced

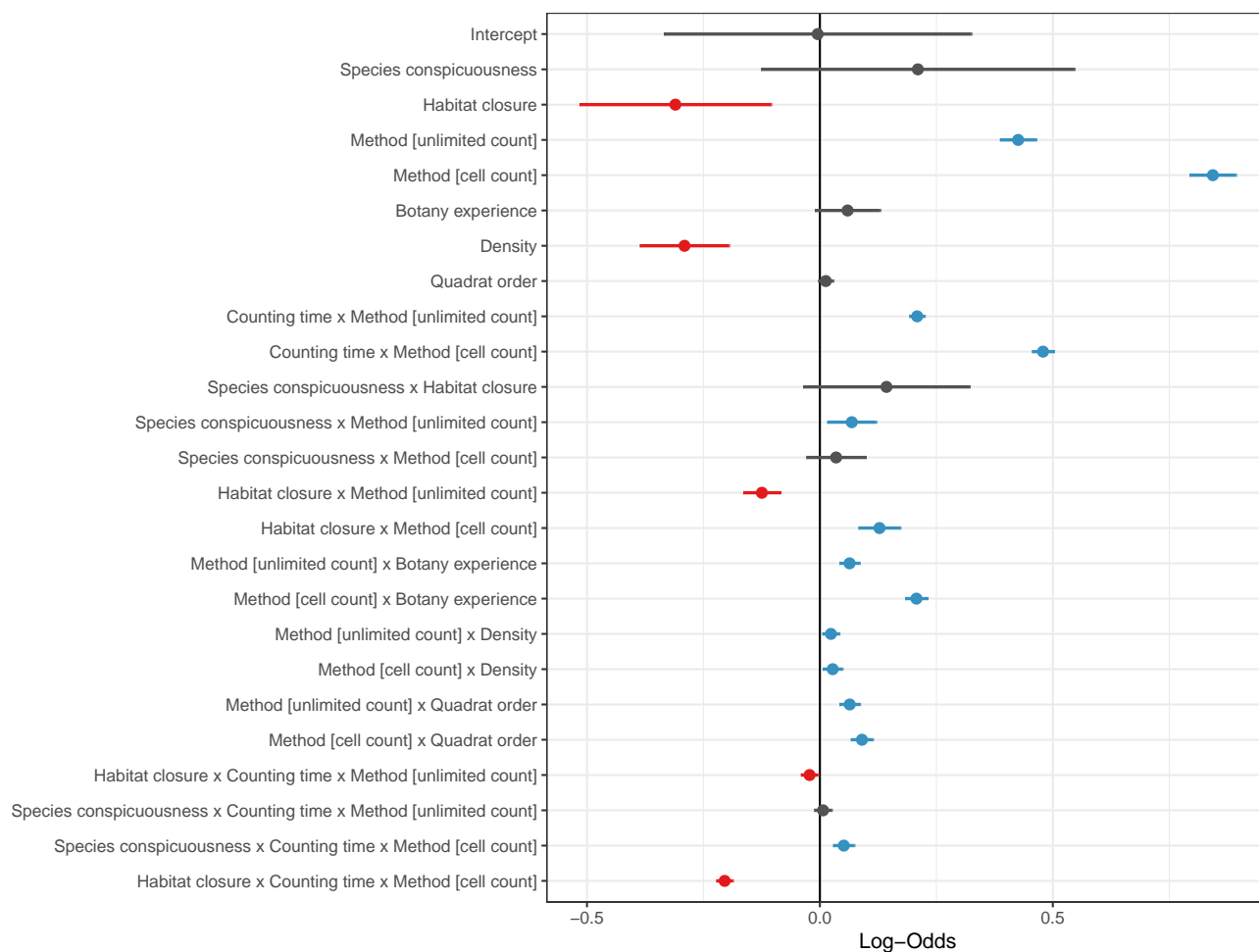


FIGURE 3.2 – Coefficients of standardised variables in the model. Dots represent estimated coefficients, and lines represent their 95% confidence intervals. Coefficients with a non-significant effect are shown in grey. The reference counting method is the quick count, in which observers had 30 seconds to estimate the number of individuals in the quadrat. The coefficients presented for the other two methods indicate the difference (on the logit scale) in mean detection probability obtained with those methods compared to the quick count. The variable ‘counting time’ appears twice because we manually coded the interaction between the counting time and the counting method, so no slope parameter is estimated for the quick count.

ced observers, and this difference was stronger for the cell count than for the unlimited count. In contrast, there was no significant correlation between experience and detection probability for the quick count. For the unlimited and cell counts, detection probability slightly increased with the position of the quadrat in the round, while there was no correlation for the quick count (Fig. 3.4).

Observers achieved higher detection probabilities with the cell count than with the unlimited count, which yielded higher detection probabilities than with the quick count. However, this came at the cost of a major increase in the time spent counting. The counting time per quadrat was fixed at 30 seconds for the quick count, and the mean counting time averaged over all sessions and observers was 1.8 minutes (ranging from 0.3 to 5.7) for the unlimited count and 8.2 minutes (from 0.9 to 21.6) for the cell count. While the time spent increased, the slope between detection probability and the other variables (e.g. observer experience, vegetation closure) was not reduced. Some variables had roughly the same correlation with detection probability regardless of the counting method (e.g. true density), while others had an even steeper slope (e.g. experience in botany).

Within the limits of the counting times we observed during the experiment, the model predicts that reaching a detection probability over 0.95 (i.e. 'almost perfect detection') is only possible by using the cell count for quadrats with a true density below 100 individuals and a counting time per quadrat of at least 20 minutes. In a very open habitat (typically with <7% vegetation cover and median vegetation height <1 cm), this can be achieved no matter the species' conspicuousness. In a less open habitat (e.g. vegetation cover <90%, median vegetation height <6 cm), the target species must be very conspicuous, i.e. a plant above 20 cm in height or 10 cm but with colourful flowers.

Substantial variation in detection probability between field sessions remained unexplained by the model, even after controlling for species and habitat characteristics, as the variance of this random effect was $\sigma_{session}^2 = 0.58$. There was also unexplained variation between quadrats ($\sigma_{quadrat}^2 = 0.42$). The unexplained between-observer variation was the smallest, with a variance of $\sigma_{observer}^2 = 0.16$. The proportion of variance explained by the model was $R_{GLMM(c)}^2 = 0.35$, and the proportion of variance explained by the model's fixed effects was $R_{GLMM(m)}^2 = 0.12$. In other words, detection

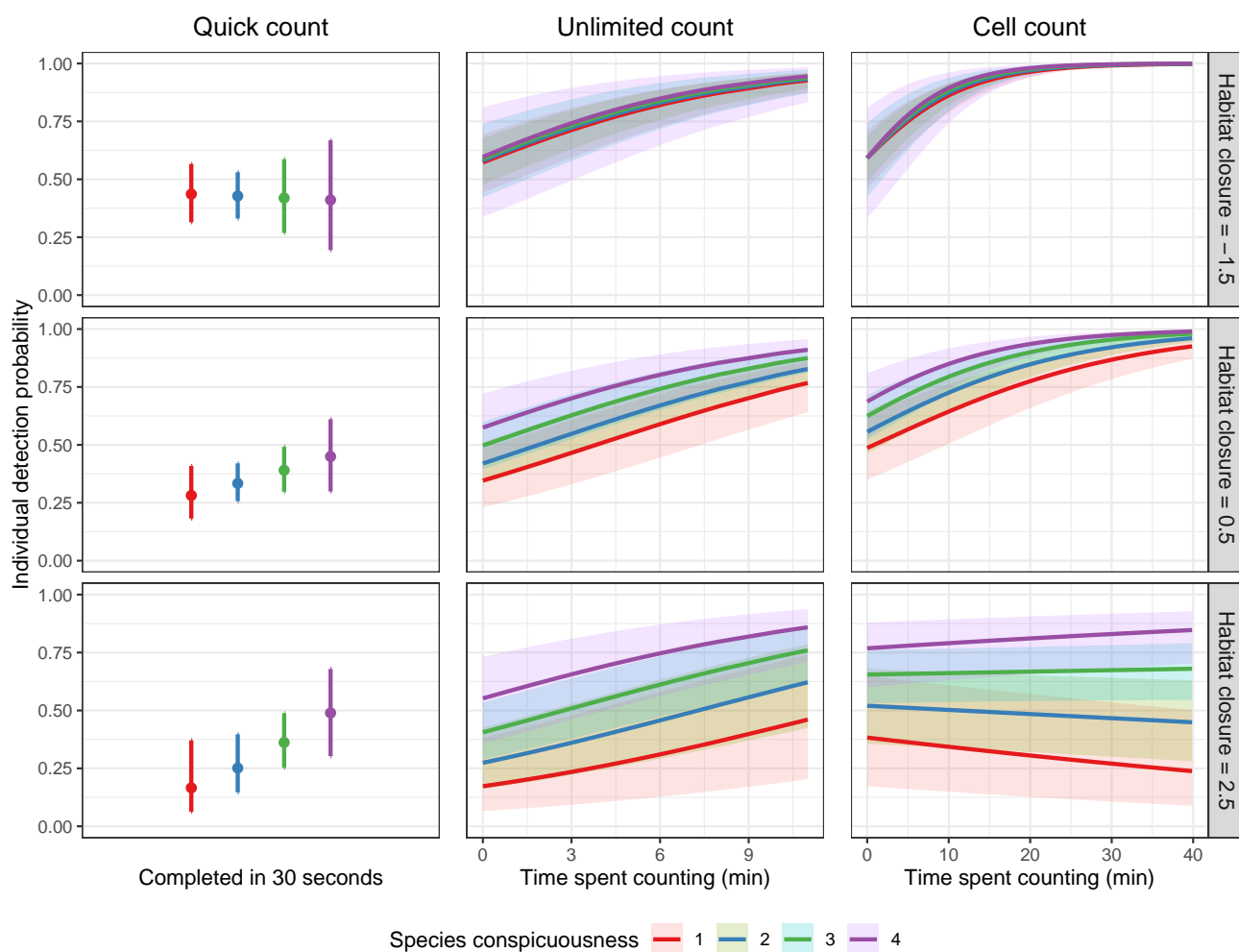


FIGURE 3.3 – Predicted detection probability depending on species conspicuousness (1 = least conspicuous; 4 = most conspicuous), habitat closure (-1.5 = most open habitats; 2.5 = most closed habitats), the counting method, and the time spent counting. Predictions were made for a quadrat containing 100 individuals of the species of interest, located in the fifth position in the round for an observer who rated his level of experience in botany at 2.5 out of 5. The maximum counting time shown for the unlimited count (11 min) and the cell count (39 min) is the maximum time an observer spent counting on a single quadrat during the experiment. Lines represent the predicted mean detection probability and the shading represents 95% confidence intervals.

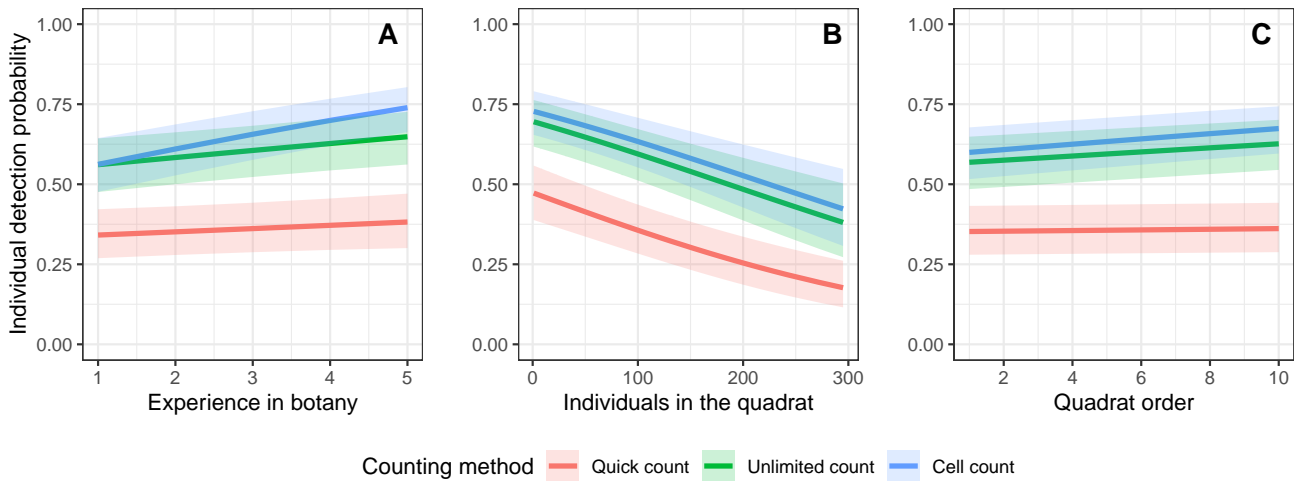


FIGURE 3.4 – Predicted detection probability of individuals, depending on the experience in botany of the observer (A), the true density (B) and the position of the quadrat in the round (C). The other variables included in the model are held constant at the following levels : species conspicuousness = 2, habitat closure = 0, quick count time = 0.5 min, unlimited count time = 3 min, cell count time = 3 min. Lines represent the mean detection probability of individuals and the shading represents 95% confidence intervals.

probability remained heterogeneous even after considering the effect of the seven variables included in the model and accounting for unexplained inter-session, inter-plot and inter-observer variance.

3.4 Discussion

This study provides the first estimate of the detection probability of individuals in plant counts, using a detection experiment with a cross-taxa and cross-habitat design. Our results demonstrated that imperfect detection is the rule when counting plants, even in small (1 m²) quadrats with unlimited counting time. Detection probability was also highly heterogeneous and varied with the species, habitat, observer and counting method. Methods involving longer survey time increased the mean detection probability, but did not achieve perfect detection, nor did they reduce the effect of the ecological and observational variables on detection probability. Even after controlling for the effects of all the variables, detection remained highly heterogeneous. Therefore, we argue that plant ecologists should not rely on the use of raw counts and should always take into account detection issues when studying plant populations.

3.4.1 Evidence for imperfect detection of plants

In our experiment, while using common plant counting methods (REISCH et al., 2018), not a single observer detected all the individuals present in all the quadrats of a field session. Even with counts unlimited in time, the predicted detection probability under average conditions (i.e. for the average values of all variables included in the model with the unlimited count) did not exceed 0.59 (95% confidence interval : 0.50–0.67). Thus, our results not only confirm that imperfect detection is the rule when counting plant individuals, but also show that detection probability can even be relatively low. Although these values may be surprising, detection issues have been previously documented for plants when searching for a species (e.g. CHEN et al., 2013), and a recent study conducted on large quadrats (20x20 m) suggested that imperfect detection may also occur for plant individuals (HAUSER et al., 2022). Furthermore, the detection probabilities we found for plants are higher than those commonly found for animals. For example, detection probabilities of 0.04–0.32 have been found in bird point counts (ROYLE, 2004), 0.07–0.41 for lizards counted along transects (KÉRY et al., 2009), 0.06–0.41 for salamanders counted along stream banks (DODD & DORAZIO, 2004), and 0.06–0.34 for freshwater mussels searched on riverbeds (CAREY et al., 2019). Nevertheless, this does not discount the fact that detection remains far from exhaustive for plants and thus should not be overlooked.

3.4.2 Effects of the ecological variables

Our results showed that species conspicuousness positively affects detection probability, while habitat closure negatively affects it. This general result was expected, as it has also been observed for plants in occupancy and time-to-detection studies (ALEXANDER et al., 2012; GARRARD et al., 2008; HAUSER et al., 2022). In open habitats, detection probability was the same regardless of the species' conspicuousness. In contrast, differences between species appeared with increasing habitat closure, reaching up to a 0.42 difference in detection probability between the extreme levels of species conspicuousness in the most closed habitats (estimated difference for the unlimited count with 3 min counting time). It shows that habitat closure drives the detection probability of plant individuals more than species conspicuousness. Furthermore, since

both species conspicuousness and habitat closure usually vary over time and space, our results show that heterogeneous detection probability is common and should be considered as the rule rather than the exception. Estimating temporal or spatial trends using raw counts when detection is heterogeneous is likely to yield biased estimates and should therefore be avoided by all means.

The negative effect of the density of individuals on detection probability was unexpected in its magnitude (e.g. a predicted detection probability of 0.67 in a quadrat with 20 individuals to 0.37 in a quadrat with 300 individuals, using the unlimited count in average conditions) and occurred regardless of the counting method. Although it would have supported our results, we did not find this phenomenon reported in the literature, even for animal taxa, where density-dependent detection probabilities usually result from changes in individual behaviour in response to density variations (VEECH et al., 2016), and not to the observer detecting fewer individuals. In our case, it may be due to the Weber–Fechner law regarding how humans perceive numbers (see NIEDER, 2020, for a summary). Indeed, studies on human cognition have shown that it becomes increasingly difficult to estimate the number of items in an area as the number grows, and that there is a general tendency to underestimate it. It is plausible that this phenomenon seldom applies to animal counts, as these do not usually involve counting immobile items in high density, as is the case for plants.

3.4.3 Observer effect

The experience in botany of observers had little effect on detection probability compared to the ecological variables and the counting time. In average conditions, the difference in detection probability between novices and the most experienced observers was 0.04 for the quick count, 0.09 for the unlimited count, and 0.17 for the cell count, and confidence intervals largely overlapped except for the cell count (Appendix 6). The advantages of having experience in botany when searching for individuals of a target species may be the ability to more quickly identify an individual once it has been detected, to make fewer identification errors, and possibly to survey the study area more efficiently by knowing where to search for the species (ARCHAUX et al., 2006). These advantages were probably minor in our experiment, since observers were trained to identify the target species before starting counts, all species were easy to identify, and

an efficient surveying strategy was of little use in 1x1 m quadrats. In this context, the observers' task can be seen as searching for small objects in a noisy environment, and it seems plausible that their performance was mainly driven by their ability to remain focused during a repetitive task, their motivation, or their fatigue during the experiment. Larger differences between observers might have been observed in larger quadrats, as the surveying strategy might then be important. Overall, it is likely that the variables we studied have a similar effect on the detection probability regardless of quadrat size. In larger quadrats, the observation process has an additional layer of complexity as observers have to walk in the quadrat and might follow different surveying strategies. Furthermore, the differences between observers might have been greater if we had involved participants with recent experience in searching for the target species (HAUSER et al., 2022) due to the well-known 'search image' effect, whereby foraging predators improve their probability of detecting the type of prey they are trained to detect (ISHII & SHIMADA, 2009). If this effect indeed applies to plant counts, population trends estimated from raw counts will be biased if the same observers always make the counts, as their detection probability will increase with time.

3.4.4 Comparison of the counting methods

As expected, increasing the survey effort, measured by the time spent counting, massively increased detection probability (ARCHAUX et al., 2006; HAUSER et al., 2022). In average conditions, the estimated detection probability was 0.36 for the quick count (30 sec counting time), 0.54 for the unlimited count (1.8 min average counting time), and 0.73 for the cell count (8.2 min). In addition, for the unlimited and cell counts, observers spending more time counting achieved a higher detection probability (e.g. for the unlimited count in average conditions, detection probability increased from 0.50 at 1 min to 0.83 at 10 min).

The gain in detection associated with counting individuals per cell instead of the whole quadrat could be due to two reasons : the cells force the observer to survey the whole surface area of the quadrat uniformly, and might also reduce uncertainty whether or not an individual has already been counted, which frequently occurs when individuals are close to each other. However, contrary to our expectations, increasing survey effort did not reduce the effect of the ecological variables on detection probability, the

most striking being the density of individuals, which had an almost identical effect on detection probability for all three counting methods.

3.4.5 Unexplained variance and implications of detection probability heterogeneity

Of the random effects included in the model, the most unexplained variation in detection probability was at the inter-session and inter-quadrat levels. Since we only measured three synthetic variables to characterise the differences between sessions and quadrats (species conspicuousness, habitat closure and true density), we expected that unexplained variance would remain at these levels. For example, we did not measure colour and height heterogeneity, for the habitat or for the target species, although these variables certainly impact detection probability (GARRARD et al., 2013; HAUSER et al., 2022).

The fact that the unexplained inter-observer variation was the lowest of the random effects is an encouraging result for future studies, as it means that there are few differences in detection probability between observers compared to the differences between species or over a habitat closure gradient. Yet, overall, more than half (65%) of the variance in detection probability remained unexplained by our model. Thus, observers had a heterogeneous detection probability between quadrats even after controlling for several variables, suggesting that factors that vary over time for each observer, such as concentration or motivation, probably explain a large part of the variation in detection probability.

3.4.6 Recommendations for counting plants

Our study shows for plants what has been documented many times for animals : that detection probability of individuals is less than one and is usually heterogeneous in space and time, regardless of the counting method and survey effort. Using counts affected by imperfect detection as a proxy for the density of individuals to make comparisons over time and space is only valid under the hypothesis of constant detection. Our findings show that multiple ecological and observational variables cause heterogeneity in detection probability. While observational variables can be standardised, it seems

unlikely that ecological variables (i.e. species conspicuousness, habitat closure and true density of individuals) will be constant in any study, even those conducted at limited temporal and spatial scales. Furthermore, trying to achieve almost perfect detection (i.e. >0.95) by increasing survey efforts to fix the issue of detection heterogeneity seems unrealistic given the resource constraints of most ecology and conservation studies. As we studied a wide variety of species and habitats, we trust that our results are transferable to most biomes and species types, provided the scientific context is comparable. The spatial scale must be equivalent in terms of quadrat size (i.e. small enough that it is not necessary to walk inside during the survey) and the studied species must be of a similar life form (e.g. herbaceous species or tree seedlings). We therefore argue that temporal or spatial trends in plant populations should not be estimated using raw counts, as they could then reflect a trend in ecological variables rather than the population's fate.

The detection probability depends on the conditions of the observation process and the studied system; thus, it has to be estimated within each study and cannot be extrapolated from our results. Several methods can be used to estimate individual detection probability, and thus estimate unbiased population sizes or trends (e.g. BUCKLAND et al., 2001; LEBRETON et al., 1992). In particular, the N-mixture method uses repeated counts of unmarked individuals on sampling units (e.g. quadrats or sites) to estimate detection probability from the differences in the number of individuals detected between counts (ROYLE, 2004). With this method, estimates of population sizes or trends are more precise if detection probability is high and homogeneous in time and space, if the mean density of individuals is high, and if the sample size, i.e. the number of sampling units and count repetitions, is high (FICETOLA et al., 2018; ROYLE, 2004). Thus, for studies using the N-mixture method, no matter the studied population and the counting method used, we recommend setting a fixed counting time as leaving it to the observer's choice will add heterogeneity to detection probability, resulting in less precise estimates.

In terms of allocating survey effort, there are three options : use a more time-consuming counting method to increase detection probability, perform more count repetitions, or survey more sampling units. The only way to be sure of the optimal design is to conduct a pilot study to estimate the mean density of individuals and their detec-

tion probability in the population of interest. However, FICETOLA et al. (2018) have shown that when the detection probability is above 0.10, the most advantageous strategy is usually to make three count repetitions and to increase the number of sampling units as much as possible. Conversely, when the detection probability is below 0.10, it is better to increase it by using a more time-consuming counting method or to increase the number of count repetitions. Thus, we recommend counting individuals in quadrats without cells with a fixed short counting time (e.g. 0.5–1 min), as this method will yield a detection probability above 0.10 for most species and allow the most sampling units to be surveyed. More time-consuming counting methods should be used only if the study population grows in a very closed habitat and the individuals are inconspicuous, or if travel costs resulting from increasing the number of sampling units is a strong constraint.

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Authors' contributions

J.P., A.B., A.C. and G.P. conceived the study and designed the methodology; J.P. and G.P. organised and conducted the field sessions; J.P. analysed the data and led the writing of the manuscript. All authors critically contributed to the drafts and gave their final approval for publication.

Data availability statement

All data and code used for this work are available from the GitHub repository : https://github.com/JanPerret/Individual_detection_in_plant_counts

Conflict of Interest statement

All authors declare no conflict of interest.

References

- ALEXANDER, H. M., SLADE, N. A., & KETTLE, W. D. (1997). Application of mark-recapture models to estimation of the population size of plants. *Ecology*, 78(4), 1230-1237. [https://doi.org/10.1890/0012-9658\(1997\)078\[1230:AOMRMT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1230:AOMRMT]2.0.CO;2) (cf. p. 131)
- ALEXANDER, H. M., REED, A. W., KETTLE, W. D., SLADE, N. A., ROELS, S. A. B., COLLINS, C. D., & SALISBURY, V. (2012). Detection and Plant Monitoring Programs : Lessons from an Intensive Survey of *Asclepias meadii* with Five Observers. *Plos One*, 7(12), e52762. <https://doi.org/10.1371/journal.pone.0052762> (cf. p. 130, 145)
- ANDRIEU, E., BESNARD, A., FRÉVILLE, H., VAUDEY, V., GAUTHIER, P., THOMPSON, J. D., & DEBUSSCHE, M. (2017). Population dynamics of *Paeonia officinalis* in relation to forest closure : From model predictions to practical conservation management. *Biological Conservation*, 215, 51-60. <https://doi.org/10.1016/j.biocon.2017.08.010> (cf. p. 131)
- ARCHAUX, F., GOSSELIN, F., BERGES, L., & CHEVALIER, R. (2006). Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science*, 17(3), 299-306. [https://doi.org/10.1658/1100-9233\(2006\)017\[0299:EOSTSR\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2006)017[0299:EOSTSR]2.0.CO;2) (cf. p. 130, 146, 147)
- ARCHAUX, F., HENRY, P.-Y., & GIMENEZ, O. (2012). When can we ignore the problem of imperfect detection in comparative studies? *Methods in Ecology and Evolution*, 3(1), 188-194. <https://doi.org/10.1111/j.2041-210X.2011.00142.x> (cf. p. 129)
- BATES, D., MAECHLER, M., BOLKER, B., WALKER, S., CHRISTENSEN, R. H. B., SINGMANN, H., DAI, B., SCHEIPL, F., GROTHENDIECK, G., GREEN, P., FOX, J., BAUER, A., & KRIVITSKY, P. N. (2022). lme4 : Linear Mixed-Effects Models using 'Eigen' and S4. (Cf. p. 137).
- BORNAND, C. N., KERY, M., BUECHE, L., & FISCHER, M. (2014). Hide-and-seek in vegetation : time-to-detection is an efficient design for estimating detectability and occurrence. *Methods in Ecology and Evolution*, 5(5), 433-442. <https://doi.org/10.1111/2041-210X.12171> (cf. p. 130)
- BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K., LAAKE, J. L., BORCHERS, D. L., & THOMAS, L. (2001). *Introduction to Distance Sampling : Estimating Abundance of Biological Populations*. Oxford University Press. (Cf. p. 149).
- BUCKLAND, S. T., MARSDEN, S. J., & GREEN, R. E. (2008). Estimating bird abundance : making methods work. *Bird Conservation International*, 18(S1), S91-S108. <https://doi.org/10.1017/S0959270908000294> (cf. p. 129)
- CAREY, C. S., JONES, J. W., BUTLER, R. S., KELLY, M. J., & HALLERMAN, E. M. (2019). A Comparison of Systematic Quadrat and Capture-Mark-Recapture Sampling Designs for Assessing Freshwater Mussel Populations. *Diversity*, 11(8), 127. <https://doi.org/10.3390/d11080127> (cf. p. 145)
- CHEN, G., KÉRY, M., PLATTNER, M., MA, K., & GARDNER, B. (2013). Imperfect detection is the rule rather than the exception in plant distribution studies. *Journal*

- of Ecology*, 101(1), 183-191. <https://doi.org/10.1111/1365-2745.12021> (cf. p. 130, 145)
- CHEN, G., KÉRY, M., ZHANG, J., & MA, K. (2009). Factors affecting detection probability in plant distribution studies. *Journal of Ecology*, 97(6), 1383-1389. <https://doi.org/10.1111/j.1365-2745.2009.01560.x> (cf. p. 130)
- DENNIS, B., MUNHOLLAND, P. L., & SCOTT, J. M. (1991). Estimation of Growth and Extinction Parameters for Endangered Species. *Ecological Monographs*, 61(2), 115-143. <https://doi.org/10.2307/1943004> (cf. p. 129)
- DODD, C. K., & DORAZIO, R. M. (2004). Using counts to simultaneously estimate abundance and detection probabilities in a salamander community. *Herpetologica*, 60(4), 468-478. <https://doi.org/10.1655/03-60> (cf. p. 145)
- ELPHICK, C. S. (2008). How you count counts : the importance of methods research in applied ecology. *Journal of Applied Ecology*, 45(5), 1313-1320. <https://doi.org/10.1111/j.1365-2664.2008.01545.x> (cf. p. 129)
- ELZINGA, C. L., & SALZER, D. W. (1998). *Measuring & Monitoring Plant Populations*. U.S. Department of the Interior, Bureau of Land Management. (Cf. p. 131).
- FICETOLA, G. F., ROMANO, A., SALVIDIO, S., & SINDACO, R. (2018). Optimizing monitoring schemes to detect trends in abundance over broad scales. *Animal Conservation*, 21(3), 221-231. <https://doi.org/10.1111/acv.12356> (cf. p. 149, 150)
- GARRARD, G. E., BEKESSY, S. A., MCCARTHY, M. A., & WINTLE, B. A. (2008). When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology*, 33(8), 986-998. <https://doi.org/10.1111/j.1442-9993.2008.01869.x> (cf. p. 130, 145)
- GARRARD, G. E., MCCARTHY, M. A., WILLIAMS, N. S. G., BEKESSY, S. A., & WINTLE, B. A. (2013). A general model of detectability using species traits. *Methods in Ecology and Evolution*, 4(1), 45-52. <https://doi.org/10.1111/j.2041-210x.2012.00257.x> (cf. p. 130, 148)
- GAUTHIER, P., PONS, V., FISOGNI, A., MURRU, V., BERJANO, R., DESSENA, S., MACCIONI, A., CHELO, C., de MANINCOR, N., DONCIEUX, A., PAPUGA, G., & THOMPSON, J. D. (2019). Assessing vulnerability of listed Mediterranean plants based on population monitoring. *Journal for Nature Conservation*, 52(125758), 1-11. <https://doi.org/10.1016/j.jnc.2019.125758> (cf. p. 131, 135)
- GAUTHIER, P., PONS, V., LETOURNEAU, A., KLESCZEWSKI, M., PAPUGA, G., & THOMPSON, J. D. (2017). Combining population monitoring with habitat vulnerability to assess conservation status in populations of rare and endangered plants. *Journal for Nature Conservation*, 37, 83-95. <https://doi.org/10.1016/j.jnc.2017.03.005> (cf. p. 131, 135)
- GILJOHANN, K. M., MCCARTHY, M. A., KEITH, D. A., KELLY, L. T., TOZER, M. G., & REGAN, T. J. (2017). Interactions between rainfall, fire and herbivory drive resprouter vital rates in a semi-arid ecosystem. *Journal of Ecology*, 105(6), 1562-1570. <https://doi.org/10.1111/1365-2745.12768> (cf. p. 131)
- HARPER, J. L. (1977). *Population Biology of Plants*. Academic Press. (Cf. p. 130).
- HARTIG, F. (2022). DHARMa : Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. (Cf. p. 137).
- HAUSER, C. E., GILJOHANN, K. M., MCCARTHY, M. A., GARRARD, G. E., ROBINSON, A. P., WILLIAMS, N. S. G., & MOORE, J. L. (2022). A field experiment characterizing variable detection rates during plant surveys. *Conservation Biology*, 36(3), e13888. <https://doi.org/10.1111/cobi.13888> (cf. p. 131, 145, 147, 148)

- ISHII, Y., & SHIMADA, M. (2009). The effect of learning and search images on predator-prey interactions. *Population Ecology*, 52(1), 27. <https://doi.org/10.1007/s10144-009-0185-x> (cf. p. 147)
- IUCN. (2019). Guidelines for Using the IUCN Red List Categories and Criteria - Version 14. (Cf. p. 129).
- KELLNER, K. F., & SWIHART, R. K. (2014). Accounting for Imperfect Detection in Ecology : A Quantitative Review. *Plos One*, 9(10), e111436. <https://doi.org/10.1371/journal.pone.0111436> (cf. p. 130)
- KENDALL, W. L., PETERJOHN, B. G., & SAUER, J. R. (1996). First-Time Observer Effects in the North American Breeding Bird Survey. *The Auk*, 113(4), 823-829. <https://doi.org/10.2307/4088860> (cf. p. 129)
- KÉRY, M., GREGG, K. B., & SCHAUB, M. (2005). Demographic estimation methods for plants with unobservable life-states. *Oikos*, 108(2), 307-320. <https://doi.org/10.1111/j.0030-1299.2005.13589.x> (cf. p. 130)
- KÉRY, M., DORAZIO, R. M., SOLDAAT, L., van STRIEN, A., ZUIDERWIJK, A., & ROYLE, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, 46(6), 1163-1172. <https://doi.org/10.1111/j.1365-2664.2009.01724.x> (cf. p. 129, 145)
- KÉRY, M., & GREGG, K. B. (2003). Effects of life-state on detectability in a demographic study of the terrestrial orchid *Cleistes bifaria*. *Journal of Ecology*, 91(2), 265-273. <https://doi.org/10.1046/j.1365-2745.2003.00759.x> (cf. p. 131)
- KÉRY, M., & SCHMIDT, B. R. (2008). Imperfect detection and its consequences for monitoring for conservation. *Community Ecology*, 9(2), 207-216. <https://doi.org/10.1556/ComEc.9.2008.2.10> (cf. p. 130)
- LEBRETON, J.-D., BURNHAM, K. P., CLOBERT, J., & ANDERSON, D. R. (1992). Modeling Survival and Testing Biological Hypotheses Using Marked Animals : A Unified Approach with Case Studies. *Ecological Monographs*, 62(1), 67-118. <https://doi.org/10.2307/2937171> (cf. p. 131, 149)
- LÜDECKE, D., AUST, F., CRAWLEY, S., & BEN-SHACHAR, M. S. (2022). ggeffects : Create Tidy Data Frames of Marginal Effects for 'ggplot' from Model Outputs. (Cf. p. 137).
- MOLANO-FLORES, B., & BELL, T. J. (2012). Projected population dynamics for a federally endangered plant under different climate change emission scenarios. *Biological Conservation*, 145(1), 130-138. <https://doi.org/10.1016/j.biocon.2011.10.022> (cf. p. 131)
- MOORE, J. L., HAUSER, C. E., BEAR, J. L., WILLIAMS, N. S. G., & MCCARTHY, M. A. (2011). Estimating detection-effort curves for plants using search experiments. *Ecological Applications*, 21(2), 601-607. <https://doi.org/10.1890/10-0590.1> (cf. p. 131)
- NAKAGAWA, S., JOHNSON, P. C. D., & SCHIELZETH, H. (2017). The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface*, 14(134), 20170213. <https://doi.org/10.1098/rsif.2017.0213> (cf. p. 137)
- NIEDER, A. (2020). The Adaptive Value of Numerical Competence. *Trends in Ecology & Evolution*, 35(7), 605-617. <https://doi.org/10.1016/j.tree.2020.02.009> (cf. p. 146)
- PETITOT, M., MANCEAU, N., GENIEZ, P., & BESNARD, A. (2014). Optimizing occupancy surveys by maximizing detection probability : application to amphibian monitoring in the Mediterranean region. *Ecology and Evolution*, 4(18), 3538-3549. <https://doi.org/10.1002/ece3.1207> (cf. p. 130)

- R CORE TEAM. (2019). R : A Language and Environment for Statistical Computing. (Cf. p. 137).
- REISCH, C., SCHMID, C., & HARTIG, F. (2018). A comparison of methods for estimating plant population size. *Biodiversity and Conservation*, 27(8), 2021-2028. <https://doi.org/10.1007/s10531-018-1522-1> (cf. p. 131, 145)
- RIPPLE, W. J., & BESCHTA, R. L. (2012). Trophic cascades in Yellowstone : The first 15 years after wolf reintroduction. *Biological Conservation*, 145(1), 205-213. <https://doi.org/10.1016/j.biocon.2011.11.005> (cf. p. 129)
- ROYLE, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, 60(1), 108-115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x> (cf. p. 131, 145, 149)
- VEECH, J. A., OTT, J. R., & TROY, J. R. (2016). Intrinsic heterogeneity in detection probability and its effect on N-mixture models. *Methods in Ecology and Evolution*, 7(9), 1019-1028. <https://doi.org/10.1111/2041-210X.12566> (cf. p. 146)
- WATSON, J., & ESTES, J. A. (2011). Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs*, 81(2), 215-239. <https://doi.org/10.1890/10-0262.1> (cf. p. 129)
- WILLIAMS, B. K., NICHOLS, J. D., & CONROY, M. J. (2002). *Analysis and Management of Animal Populations : Modeling, Estimation, and Decision Making*. Academic Press. (Cf. p. 129).
- YOCCOZ, N. G., NICHOLS, J. D., & BOULINIER, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16(8), 446-453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4) (cf. p. 129)



Pavot de Lapeyrouse (*Papaver lapeyrouseanum*), massif du Carlit, août 2020.

Discussion générale

0.6 Perspectives de la thèse pour la recherche

Les développements méthodologiques que je juge prioritaires ou particulièrement prometteurs pour améliorer le suivi des populations de plantes ont en partie été présentés dans la discussion du premier chapitre de cette thèse. Dans la présente partie de la discussion générale, je vais en premier lieu revenir plus en détail sur l'amélioration des plans d'échantillonnage, puis sur l'amélioration de la prise en compte des erreurs d'observation. Dans un troisième temps, j'aborderai les axes de recherche méthodologique qui ne se rapportent ni à l'échantillonnage ni aux erreurs d'observation, c'est-à-dire l'utilisation d'images prises avec des drones, la banque de graine et l'intégration de données issues de plusieurs processus d'observations dans le même modèle statistique.

0.6.1 Axes de recherche pour améliorer la précision des estimations de taille et de tendance des populations végétales grâce aux plans d'échantillonnage

Dans le deuxième chapitre de cette thèse, j'ai présenté une méthode pour améliorer la précision des estimations de taille de population lorsque les individus sont spatialement agrégés. Les méthodes d'échantillonnage que j'ai étudiées étaient uniquement des méthodes d'échantillonnage à une étape, qui sont plus faciles à mettre en œuvre sur le terrain que les méthodes d'échantillonnage adaptatif. Cependant, certaines de ces méthodes, comme l'*Adaptive Cluster Sampling* (ACS; THOMPSON, 1990), ont été développées spécifiquement pour améliorer la précision des estimations de tailles de population lorsque les individus sont agrégés. Ces méthodes ont fréquemment été utilisées pour estimer des tailles de population (TURK & BORKOWSKI, 2005), mais très rarement pour estimer des tendances temporelles (voir cependant SHACKLETON et al., 2020). Le gain de précision que ces méthodes pourraient permettre d'obtenir pour l'estimation de tendances temporelles est largement inconnu. Réaliser une étude de simulation similaire à celle présentée dans le chapitre 2 permettrait de déterminer si ces méthodes peuvent permettre d'obtenir plus de précision que les méthodes d'échantillonnage en une étape, et dans quelles circonstances cela est possible (par exemple selon la densité d'individus de la population, leur niveau d'agrégation, le coût de la distance à parcou-

rir entre les unités d'échantillonnage, etc.). Par ailleurs, il semble fréquent qu'il y ait plusieurs niveaux d'agrégation dans les populations de plantes (LARA-ROMERO et al., 2016; SEABLOOM et al., 2005). Concevoir des plans d'échantillonnage emboîtés à plusieurs échelles spatiales pourrait permettre de s'adapter à ce type de situation (LARK & CORSTANJE, 2009; WEBSTER et al., 2006), et à certaines de ces échelles spatiales l'échantillonnage pourrait être adaptatif. La précision que ce type de plan d'échantillonnage permet d'obtenir est actuellement inconnue. Ici également, des études de simulation permettraient de comprendre dans quelles situations ce type de plan d'échantillonnage est performant. Néanmoins, les patrons d'agrégation que peuvent avoir les populations de plantes selon l'échelle spatiale sont mal connus. Améliorer préalablement les connaissances dans ce domaine permettrait de calibrer les simulations de manière plus réaliste, et ainsi garantir que les résultats soient bien transposables à la réalité. En outre, les méthodes d'échantillonnage adaptatif ont des désavantages qui les rendent parfois difficiles à mettre en œuvre sur le terrain, comme le fait que la taille d'échantillon finale ne soit pas connue avant la fin de la phase de terrain (du moins pour l'ACS). En plus des études de simulation, il sera nécessaire de réaliser des tests sur le terrain pour s'assurer que la méthode soit réaliste à mettre en œuvre et qu'elle reste avantageuse par rapport aux méthodes d'échantillonnage à une étape malgré cette contrainte.

Un autre axe de développement des méthodes d'échantillonnage est leur adaptation aux situations où la population statistique « se déplace » dans l'espace. Par exemple, si l'objectif d'un suivi est d'estimer le nombre d'individus dans un site donné, une approche classique est de tirer un échantillon d'unités spatiales au sein de ce site et d'y compter le nombre d'individus chaque année. La répétition du suivi sur les mêmes unités est le plus précis statistiquement pour estimer les tendances (URQUHART, 2012). Cependant, si l'habitat favorable de l'espèce se déplace, les individus vont progressivement disparaître des unités de l'échantillon de départ, et un déclin de population sera observé, alors qu'il est possible que le nombre d'individus soit stable ou en augmentation dans la zone grâce à la colonisation de nouvelles surfaces d'habitat favorable. Ce type de situation risque de se présenter de plus en plus fréquemment à cause du changement climatique, qui engendre des déplacements latitudinaux et altitudinaux des espèces (LENOIR et al., 2008; VITASSE et al., 2021). Pourtant, il n'existe pour le moment pas de méthode d'échantillonnage adaptée à ce type de situation. Il est donc urgent

de développer ce type de méthode. Plusieurs approches sont envisageables pour obtenir des estimations non biaisées des tendances de population dans ce type de situation, comme par exemple estimer la probabilité d'apparition de nouvelles unités spatiales d'habitat favorable et la probabilité de colonisation de ces unités.

Un troisième axe de développement méthodologique est l'adaptation des stratégies d'échantillonnage temporelles aux tendances de population non linéaires, et notamment aux tendances non-monotones. Durant mon doctorat, j'ai travaillé uniquement sur l'estimation de tendances de population linéaires. Avec cet objectif, l'éventuelle non-linéarité des tendances est un facteur de nuisance, puisqu'il ajoute du bruit par rapport à la tendance de fond que l'on cherche à estimer. Cependant, comprendre la dimension non-linéaire des tendances peut permettre d'éviter que la tendance estimée ne soit un artefact dû à l'année de référence (DUCHENNE et al., 2022). Elle peut également améliorer l'interprétation écologique des tendances, et ainsi permettre d'améliorer la conservation des populations (RIGAL et al., 2020).

0.6.2 Axes de recherche pour améliorer la prise en compte des erreurs d'observation

Comme je l'ai présenté dans le chapitre 1 de cette thèse, les erreurs d'observation sont actuellement ignorées dans la majorité des suivis de populations de plantes, bien qu'un changement semble avoir été amorcé, comme en témoignent le développement des modèles de Time-to-Detection occupancy (GARRARD et al., 2008) et de Zero-augmented beta error (WRIGHT et al., 2017) spécifiquement pour les plantes. Améliorer la prise en compte des erreurs d'observation nécessite de faire des recherches méthodologiques pour tester les méthodes existantes et, si nécessaire, les adapter ou en développer de nouvelles. Cependant, il convient surtout à ce stade d'attirer l'attention des botanistes sur le problème des erreurs d'observation et de leur faire connaître les méthodes permettant de les prendre en compte afin de faire évoluer les pratiques. J'espère que les articles constituant les chapitres 1 et 3 de ce manuscrit participeront à agir dans ce sens. Cependant, des articles montrant que la détection est imparfaite chez les plantes ont régulièrement été publiés depuis le début des années 1990, et cela ne semble pas avoir fait radicalement évoluer les pratiques (ALEXANDER et al., 1997; CHEN et

al., 2013; CHEN et al., 2009; KÉRY et al., 2005). Pour appuyer le message que les erreurs d'observation peuvent vraiment fausser les résultats d'une étude, un moyen serait de réanalyser les données d'études où la probabilité de détection a été estimée, mais cette fois sans l'estimer. Étant donné les probabilités de détection relativement faibles qui sont reportées dans certaines études, les interprétations écologiques des résultats seront certainement différentes. Autrement dit, cela permettra de montrer que les auteurs n'auraient pas eu les mêmes conclusions s'ils n'avaient pas estimé la probabilité de détection.

Comme je l'ai détaillé dans le chapitre 1, plusieurs méthodes qui permettent d'estimer la probabilité de détection n'ont encore jamais été utilisées sur les plantes alors qu'elles sont a priori parfaitement adaptées. C'est par exemple le cas de la méthode N-mixture (ROYLE, 2004) et de la méthode TTD-N-mixture (STREBEL et al., 2021). Une manière d'aider à faire changer les pratiques des botanistes vis-à-vis des erreurs de détection est de réaliser des études méthodologiques sur ces méthodes dans lesquelles elles sont utilisées pour estimer des valeurs connues. Par exemple, cela peut consister à utiliser la méthode N-mixture pour estimer le nombre d'individus présents dans un quadrat où cette valeur est connue avec certitude, soit car ils y ont été placés expérimentalement (comme dans HAUSER et al., 2022) ou car cette valeur est mesurable avec certitude grâce à une autre méthode de mesure (**perret_plants_2022**). Ce type d'étude permettra de vérifier que les méthodes étudiées permettent bien d'obtenir des estimations non biaisées sur les plantes, de tester leurs performances et de faire des recommandations pour leur utilisation pour le suivi de populations végétales. Pour les modèles N-mixture, les données de l'expérimentation présentée dans le chapitre 3 de cette thèse pourraient servir de base à ce type d'étude, car je dispose à la fois de comptages répétés par différents observateurs sur chaque quadrat et du nombre « réel » d'individus. Après ces études méthodologiques, l'étape suivante est de réaliser et publier des études qui utilisent ces méthodes mais dont le sujet principal n'est pas méthodologique. Cela permettra de faire connaître les méthodes à un plus large public, et de montrer des exemples de cas concrets où elles ont été utilisées avec succès.

Une piste pour réduire les erreurs d'observation que je n'ai pas explorée durant mon doctorat est l'utilisation de l'entraînement avec rétroaction correctrice (*feedback*

training en anglais) pour entraîner les observateurs à prendre les mesures. En effet, de nombreuses mesures que nous utilisons pour suivre les populations de plantes sont des mesures que nous estimons de manière visuelle, comme par exemple le taux de recouvrement d'une espèce. Mais pour bon nombre de ces mesures nous n'avons jamais de correction, puisque la valeur réelle de la variable que l'on mesure ne peut pas être mesurée sur le terrain. Le calibrage de notre manière de mesurer se fait donc généralement en comparant nos mesures à celles d'autres observateurs, qui peuvent être tout aussi biaisées que les nôtres. Entraîner les observateurs avec un dispositif virtuel dans lequel ils peuvent avoir accès à la vraie valeur de ce qu'ils mesurent pourrait leur permettre de se corriger au fur et à mesure et ainsi améliorer la précision et réduire le biais de leurs mesures. De plus, cela pourrait permettre de réduire les différences inter-observateurs, puisque tous les observateurs s'entraîneraient de la même manière, et ce même dans le cadre d'études à large échelle où tous les observateurs ne peuvent pas se rencontrer et calibrer leurs mesures ensemble. Ce type de dispositif d'entraînement virtuel a déjà été utilisé avec succès pour améliorer la précision de comptages d'oiseaux (ERWIN, 1982), et la précision d'estimations visuelles de dommages causés aux feuilles par des herbivores (XIROCOSTAS et al., 2022). En outre, les informations collectées durant l'entraînement des observateurs pourraient servir pour améliorer les estimations de l'effet observateur dans le cadre d'études réalisées sur de grandes échelles spatiales, où tous les observateurs ne peuvent pas faire des passages répétés sur des unités prospectées par d'autres observateurs. Ces informations pourraient être incorporées en créant plusieurs classes d'observateurs selon les résultats obtenus durant l'entraînement virtuel (par exemple observateur bon, moyen ou mauvais) et en traitant cela comme une covariable caractérisant les observateurs, ou alors en utilisant leurs scores durant l'entraînement comme un prior informatif dans un cadre bayésien.

Dans les chapitres 2 et 3 de cette thèse, j'ai travaillé uniquement sur les comptages d'individus dans le but d'estimer des tailles de population ou des tendances de la densité d'individus. Cependant, dans un contexte de conservation, il est possible que l'objectif d'un suivi soit simplement d'obtenir un « indicateur de tendance » d'une population sans qu'une variable d'état particulière ne soit visée (CASNER et al., 2014; NOON et al., 2012; TEMPEL & GUTIERREZ, 2013). Par exemple, la liste rouge de l'IUCN se base soit sur des critères de taille de population, soit sur des critères de surface de l'aire de

distribution (IUCN, 2019). Dans ce cas, la variable d'état à suivre et la métrique à utiliser peuvent être choisies en fonction de critères de puissance statistique, c'est-à-dire pour quelle variable d'état et avec quelle métrique il sera possible de détecter le plus tôt une tendance de population d'une magnitude donnée avec le même effort de terrain. La performance relative des différents choix possibles dépend alors de plusieurs facteurs : la relation entre les variables d'état (par exemple un déclin de densité d'individus peut avoir lieu sans qu'il n'y ait de déclin du taux de recouvrement, et vice-versa), le coût des mesures selon la métrique choisie (par exemple des estimations visuelles du taux de recouvrement demandent généralement moins de temps que des comptages d'individus, ce qui permet d'augmenter le nombre d'unités spatiales prospectées pour le même budget), et la précision des mesures selon la métrique et la méthode de mesure utilisées (par exemple des estimations visuelles de taux de recouvrement risquent d'être plus variables que des comptages d'individus). La puissance statistique qui pourra être obtenue en fonction de ces choix pour les populations de plantes est actuellement largement inconnue. Pour fournir des recommandations concernant ces choix, il est nécessaire de réaliser des suivis de population où plusieurs métriques sont mesurées sur toutes les unités spatiales. L'acquisition de ces données peut être relativement lourde, et je n'ai pas connaissance de jeux de données existants de ce type. Une « expérimentation distribuée » (*coordinated distributed experiment* en anglais ; FRASER et al., 2013) serait idéale pour constituer ce type de jeu de données sur des gradients importants d'espèces, d'environnements et d'observateurs. Par ailleurs, durant l'expérimentation présentée dans le chapitre 3 de cette thèse, les observateurs ont mesuré le temps jusqu'à détection et le taux de recouvrement de l'espèce en plus des trois méthodes de comptage (données non présentées dans l'article), et le comptage du nombre d'individus par cellule permet de connaître le pourcentage de sous-unités occupées, c'est-à-dire une mesure de site occupancy à fine échelle spatiale. Comparer les variances de chaque métrique dans ce jeu de données pourrait permettre d'avoir une idée grossière de leur performance relative. Néanmoins, la comparaison des métriques pose un problème d'interprétation, puisqu'un déclin de nombre d'individus et un déclin de taux de recouvrement n'ont pas nécessairement le même sens biologiquement parlant (voir par exemple FRECKLETON et al., 2005).

Finalement, l'une des perspectives de recherche de cette thèse en rapport avec les

erreurs d'observation concerne la cognition humaine. Dans le chapitre 3, nous avons vu que malgré un modèle incluant un grand nombre de variables, d'interactions entre variables et d'effets aléatoires (observateur, session et quadrat), environ 65% de la variance de la probabilité de détection restait inexplicée par le modèle. Cela suggère qu'une grande partie de l'hétérogénéité de la probabilité de détection vient de facteurs qui varient au cours du temps, comme la concentration de l'observateur ou sa motivation. Dans le cadre des études que nous réalisons en écologie et notamment des suivis de population, les différences de mesures moyennes entre observateurs, que l'on appelle souvent « l'effet observateur », sont un paramètre de nuisance, puisqu'elles ajoutent du bruit par rapport au signal que l'on cherche à estimer. Il est donc courant d'ajouter une variable « observateur » dans les modèles statistiques afin d'estimer avec plus de précision les paramètres d'intérêt, mais les phénomènes cognitifs qui génèrent cet effet sont mal compris. Comprendre ces phénomènes et ainsi pouvoir décomposer l'effet observateur permettrait de pouvoir le réduire avec de l'entraînement si certains des phénomènes impliqués peuvent être réduits de cette manière, ou en adaptant l'organisation du travail de terrain pour limiter les phénomènes de fatigue. Par ailleurs, d'un point de vue purement cognitif, comprendre quels phénomènes constituent l'effet observateur pourrait contribuer à mieux comprendre les différences de perception de la nature et plus généralement de notre environnement qu'il y a entre les gens (voir par exemple GÄRLING & GOLLEDGE, 1989).

0.6.3 Autres axes de recherche pour améliorer le suivi des populations de plantes

Un premier développement méthodologique prometteur est l'utilisation de drones équipés d'une caméra pour effectuer des suivis d'espèces de plantes herbacées, que ce soit au niveau populationnel ou individuel. Des études ont déjà démontré la faisabilité de cette approche, mais la détection des individus sur les images y était faite par un observateur humain, ce qui limite fortement la quantité d'images pouvant être analysées (voir notamment ROMINGER et al., 2021). L'utilisation de drones serait particulièrement prometteuse si elle était couplée avec une détection automatique des individus avec des méthodes de machine learning, car une telle approche permettrait de lever la limite de la quantité d'images analysables par des observateurs humains. Cependant, avant que

ce type d'approche puisse être utilisé pour des suivis de population à large échelle, il sera nécessaire de conduire des tests dans un grand nombre de conditions (gradient de visibilité de l'espèce recherchée, gradient de fermeture de l'habitat, etc.). Cela permettra d'évaluer la quantité d'erreurs d'observation générées par cette approche selon les conditions, de déterminer en quelle mesure il est possible de les corriger statistiquement (voir DAMGAARD, 2021), et ainsi de savoir dans quelles conditions l'augmentation de la surface observée grâce à l'automatisation permet d'obtenir des estimations plus précises et non biaisées des tailles et des tendances de population.

Un deuxième axe de développement méthodologique important est l'estimation de l'état de la banque de graines dans le cadre de suivis populationnels. La banque de graines est un élément central du cycle de vie de beaucoup d'espèces de plantes, notamment pour les espèces annuelles. Elle joue un rôle essentiel dans la viabilité des populations, leur diversité génétique et leurs capacités d'adaptation (THOMPSON et al., 1997). Pour de nombreuses espèces pionnières, il est courant d'observer des disparitions de populations pendant de nombreuses années et des réémergences spectaculaires à la suite de perturbations (GAZAIX et al., 2020). Pourtant, la banque de graines n'est presque jamais prise en compte dans les suivis populationnels. Une des raisons de cela est certainement que, pendant longtemps, la seule façon d'étudier la banque de graines était de l'observer directement en collectant des échantillons de sol et en triant les graines qu'ils contiennent, ou en mettant les échantillons de sol dans des conditions propices à la germination pour que la banque de graines s'exprime (THOMPSON & GRIME, 1979). Des méthodes statistiques ont été développées durant la dernière décennie pour estimer des variables d'état relatives à la banque de graine avec des modèles de Markov cachés (*Hidden Markov Model* en anglais; FRÉVILLE et al., 2013; LE COZ et al., 2019). Au départ ces méthodes ne s'appliquaient qu'à des situations particulières de métapopulations, mais elles ont par la suite été étendues à d'autres structures de populations, et des applications ont été faites sur des suivis de plantes messicoles (PLUNTZ et al., 2018). Pour le moment ces méthodes n'ont jamais été utilisées pour des suivis d'espèces à enjeux de conservation, alors que de nombreuses espèces menacées sont des espèces pionnières pour lesquelles avoir des informations sur la banque de graines serait d'une grande valeur pour mieux interpréter les tendances de population et améliorer les actions de conservation. Pour cela il est nécessaire de mener des études afin de vérifier

que ces méthodes fonctionnent dans un contexte de conservation, où l'hétérogénéité entre sites et la variabilité temporelle des observations sera probablement plus élevée que dans les exemples d'application existants.

Un troisième axe de développement méthodologique est l'intégration de données issues de processus d'observation différents dans le même modèle et l'utilisation des modèles intégrés de population (BESBEAS et al., 2002), qui n'ont à ma connaissance encore jamais été utilisés sur les plantes. Cette famille de méthodes statistiques a donné lieu à des développements méthodologiques particulièrement féconds depuis 20 ans (SCHAUB & ABADI, 2011; ZIPKIN & SAUNDERS, 2018). Au départ cela servait essentiellement à améliorer la précision des estimations dans des situations où peu de données étaient disponibles, ou pour l'étude d'espèces particulièrement rares ou discrètes. Mais les nombreux développements qui ont été réalisés permettent maintenant d'utiliser ces méthodes pour répondre à des questions d'écologie jusque-là restées sans réponse faute de méthodes adaptées (voir par exemple QUÉROUÉ et al., 2021). Elles pourraient ainsi permettre d'améliorer la précision des estimations de tendances de population sans nécessairement augmenter le coût des études, et de mieux comprendre les processus démographiques complexes sous-jacents à la dynamique de certaines populations de plantes menacées. L'intégration de données de natures différentes dans le même modèle statistique me semble particulièrement prometteuse pour améliorer la précision des estimations de probabilité d'occupancy car des méthodes ont été développées pour intégrer des données collectées selon un protocole formalisé et des observations opportunistes (*presence-only data* en anglais), qui sont souvent très abondantes pour les plantes (KOSHKINA et al., 2017). Par ailleurs, je pense que des jeux de données déjà existants pourraient permettre de tester les modèles de population intégrés sur des espèces de plantes, comme par exemple pour le Chardon bleu des Alpes, *Eryngium alpinum*, où des données de suivi démographique individuel et de suivis par comptage existent déjà pour les Alpes françaises (pour le suivi démographique, voir ANDRELLO et al., 2012). Cela permettrait d'évaluer la performance de ces méthodes à moindre coût, ainsi que de vérifier si elles nécessitent des adaptations spécifiques aux populations de plantes. Par ailleurs, des variables d'état relatives à la banque de graines pourraient être estimées au sein d'un modèle de population intégré et utilisant à la fois l'information venant des observations faites au niveau de la population et des observations faites au

niveau individuel.

0.7 Perspectives de la thèse pour la conservation de la flore

Dans le chapitre 1 de cette thèse, j'ai présenté une synthèse des connaissances sur les méthodes de suivi des populations de plantes, et identifié les sujets de développement méthodologique qui me semblaient les plus prometteurs. Dans le chapitre 2, j'ai proposé une manière d'adapter les plans d'échantillonnage à l'agrégation des individus de la population étudiée, ce qui permet de substantiellement améliorer la précision des estimations de taille de population. Dans le chapitre 3, j'ai montré que la détection imparfaite est la règle et non l'exception lorsque l'on compte des individus non marqués, et que la probabilité de détection varie en fonction de variables observationnelles (temps de comptage, expérience de l'observateur) mais également de variables écologiques (visibilité de l'espèce, fermeture de l'habitat, densité d'individus). La probabilité de détection est donc certainement hétérogène dans le temps et l'espace dans le contexte de la plupart des suivis de population, car ces variables écologiques sont généralement hétérogènes temporellement et spatialement. Il est donc nécessaire d'estimer la probabilité de détection des individus pour éviter d'obtenir des estimations biaisées des tailles et des tendances de populations. L'étude présentée dans le chapitre 3 a également permis de faire des recommandations sur comment améliorer les méthodes de comptage afin de réduire la variabilité inter-observateur des mesures. Les chapitres 2 et 3 de cette thèse ont donc des implications opérationnelles claires qui permettront d'améliorer la précision et de réduire le biais des estimations de taille et de tendance des populations de plantes.

Dans le chapitre 1 de cette thèse, j'ai mis en évidence que les méthodes permettant d'estimer les erreurs d'observation sont peu utilisées dans la littérature scientifique sur les plantes, confirmant ce qui avait déjà été montré avec une revue quantitative de la littérature par KELLNER et SWIHART (2014). Il s'agit d'une image basée majoritairement sur des suivis réalisés par des chercheurs académiques, complétée probablement de quelques suivis réalisés par des acteurs non-académiques ayant fait l'objet d'une pu-

blication scientifique. Il est difficile de se faire une idée précise des pratiques de suivi en dehors de la recherche académique, car ceux-ci font rarement l'objet de publications (voir cependant JAILLOUX, 2010 ; MARSH & TRENHAM, 2008). Néanmoins, la majorité des suivis de population (et d'ailleurs des actions de conservation) sont réalisés par des acteurs non académiques. Pour améliorer la conservation de la flore, il est donc crucial d'améliorer les suivis réalisés en dehors de la recherche académique et d'identifier les problèmes rencontrés par les acteurs non-académiques de la conservation. Pour ce qui concerne les suivis réalisés en dehors de la recherche académique, je ne connais que la situation en France alors je parlerai spécifiquement du cas français par la suite, bien qu'il semble que la situation soit relativement similaire dans d'autres pays (MARSH & TRENHAM, 2008).

0.7.1 État des pratiques de suivi des populations de plantes par les acteurs de la conservation non-académiques en France

Je ne dispose pas de données quantifiées sur l'état des pratiques de suivi en dehors de la recherche académique, mais je pense avoir une relativement bonne vue d'ensemble des suivis réalisés actuellement en France. En effet, j'ai discuté de ce sujet avec un grand nombre d'acteurs non-académiques de la conservation avant et durant mon doctorat, grâce aux moyens suivants :

1. J'ai suivi un Master qui forme des professionnels de la gestion d'espaces naturels et de l'expertise naturaliste, et j'ai fait mes trois stages de Master dans le domaine de la gestion d'espaces naturels (Parc Naturel Régional, Réserve naturelle et Office National des Forêts). Les suivis de population étaient un sujet de discussion régulier au cours de mes stages, et une grande partie de mes amis et camarades d'études travaillent actuellement dans la gestion d'espaces naturels. Connaissant mon sujet de thèse, ils m'ont régulièrement contacté pour avoir des conseils pour la conception de suivis qu'ils allaient mettre en place ou un avis sur un suivi existant.
2. Au début de mon doctorat, j'ai organisé une journée de discussion avec une quarantaine de professionnels de la conservation de la flore afin d'échanger sur leurs pratiques et sur les problèmes qu'ils rencontrent avec les suivis de population.

J'ai par la suite continué à échanger avec certains d'entre eux.

3. Durant mon doctorat j'ai réalisé une expérimentation de terrain (chapitre 3) qui a réuni 167 participants, dont une grande partie étaient des acteurs de la conservation de la flore. Au cours de ces journées passées sur le terrain, nous avons souvent discuté des suivis qu'ils mettent en oeuvre et des problèmes rencontrés.
4. Depuis juillet 2020 je participe à un groupe de travail mis en place par l'Office Français de la Biodiversité (OFB), dont l'objectif est de réfléchir à la future stratégie nationale de suivi de la flore. Cette stratégie devra comporter un volet de surveillance de la flore commune et un volet de suivi des espèces rares et menacées. Les méthodes de suivis de divers acteurs sont régulièrement discutées au sein du groupe de travail.

Les discussions que j'ai eues dans ces différents contextes m'ont amené à faire les constats suivants :

1. Les suivis de population de plantes réalisés par les acteurs de la conservation français ne se basent pas toujours sur un échantillonnage probabiliste. Je ne suis pas capable d'en estimer précisément la proportion, mais je pense que les suivis basés sur de l'échantillonnage de jugement sont majoritaires. Je tiens néanmoins à signaler que j'ai régulièrement entendu parler de suivis basés sur de l'échantillonnage probabiliste (voir par exemple l'observatoire de la flore de Bourgogne ; FEDOROFF, 2009).
2. Très peu de suivis incluent une estimation des erreurs d'observation. Il est courant que les personnes qui conçoivent les protocoles de suivi aient mis en place des stratégies pour réduire les erreurs d'observation. Par exemple, des comparaisons de méthodes de mesure sont souvent faites au début des programmes de suivi pour déterminer quelle méthode est la plus pratique à mettre en oeuvre et quelle méthode semble donner les résultats les plus reproductibles. Cependant, ce type de test ne permet que de comparer les mesures prises avec différentes méthodes entre elles, et non de les comparer à la valeur réelle de ce qui est mesuré. L'importance des erreurs d'observation reste donc inconnue. En dehors des programmes pilotés par des chercheurs académiques, je n'ai entendu parler d'aucun programme de suivi de population de plantes mis en oeuvre en France dans lequel les erreurs d'observation sont estimées. L'adoption des méthodes permettant de

faire cela est encore faible parmi les chercheurs académiques (voir chapitre 1 et KELLNER & SWIHART, 2014), et je pense qu'elle est encore plus faible parmi les acteurs de la conservation français.

3. Les suivis de populations de plantes réalisés en France sont mis en œuvre par une grande diversité de structures, comme les conservatoires botaniques, des gestionnaires d'espaces naturels, des associations de protection de l'environnement, des bureaux d'étude, et des naturalistes réalisant des suivis de manière autonome. Les personnes mettant en œuvre les suivis sur le terrain ont également des profils très divers, notamment en ce qui concerne le niveau de formation sur les questions méthodologiques. Pour prendre des exemples extrêmes, certaines de ces personnes ont fait un doctorat en écologie et lisent régulièrement les publications scientifiques sur les derniers développements méthodologiques du domaine, et d'autres n'ont pas fait d'études d'écologie et sont simplement des naturalistes passionnés qui réalisent des suivis bénévolement sur leur temps libre. Par ailleurs, l'activité de suivi est fortement décentralisée, et personne ne sait exactement quelles espèces sont suivies, où, par qui, et avec quelles méthodes. Une grande partie des personnes qui conçoivent les protocoles de suivi ou les mettent en œuvre sur le terrain le font de manière autonome, et communiquent peu avec les autres personnes réalisant cette activité en dehors de leurs collègues directs. Cela rend les retours d'expérience et les échanges de bonnes pratiques difficiles. Je tiens toutefois à signaler que cette situation semble être en train de changer, et plusieurs recensements des suivis qui sont réalisés sont en cours à différentes échelles spatiales (Flore sentinelle pour les Alpes, RESEDA-Flore pour le bassin méditerranéen, le groupe de travail flore de l'OFB au niveau national). La forte décentralisation de l'activité de suivi, la diversité des structures et des personnes impliquées, et le manque de communication entre celles-ci, sont des difficultés importantes pour faire évoluer les pratiques. Le fait que l'activité de suivi soit fortement décentralisée et que cela rende difficile de faire évoluer les pratiques n'est pas une spécificité française ; c'est également le cas aux États-Unis et probablement dans de nombreux autres pays (MARSH & TRENHAM, 2008).

Faire évoluer les pratiques des acteurs de la conservation demandera du temps. Je pense qu'accompagner et autant que possible faciliter cette évolution fait partie du rôle

des chercheurs en biologie de la conservation. Pour cela, la première étape est de sensibiliser le maximum d'acteurs réalisant des suivis aux problèmes posés par l'échantillonnage de jugement et les erreurs d'observation, par exemple en faisant des présentations sur le sujet lors d'événements réunissant de nombreux acteurs. La deuxième étape est de proposer davantage de formations sur ces sujets afin que les acteurs de la conservation intéressés puissent prendre en compte ces problèmes dans leurs futurs suivis. Pour que ces formations soient efficaces, je pense qu'il faut limiter les prérequis statistiques nécessaires et mettre l'accent sur les aspects opérationnels pour que les connaissances acquises soient rapidement applicables. De telles formations sont déjà proposées par l'Atelier Technique des Espaces Naturels (ATEN), qui a été intégré à l'AFB en 2017 puis l'OFB en 2019, et des diplômes de haut niveau accessibles aux professionnels en formation continue sont proposés par l'École Pratique des Hautes Études (EPHE). La troisième étape est d'accompagner les acteurs motivés dans la conception de protocoles de suivi qui se basent sur de l'échantillonnage probabiliste et qui permettent d'estimer les tendances de population de manière robuste et au moindre coût. Cela permettra de leur faciliter la conception des protocoles et de leur éviter des erreurs inhérentes à l'apprentissage de nouvelles méthodes. La quatrième étape est de communiquer les résultats de ces suivis auprès du plus grand nombre possible d'acteurs de la conservation, éventuellement par l'intermédiaire de publications scientifiques, mais surtout au travers de présentations orales lors d'événements regroupant de nombreux acteurs de la conservation. En effet, je suis persuadé que montrer des exemples d'études qui ont fonctionné, pour lesquelles l'utilisation de meilleures méthodes a permis d'avoir des résultats plus fiables et de réduire le risque de prendre de mauvaises décisions de conservation, est un puissant levier pour décider des acteurs réticents à changer leurs pratiques. La dernière étape est de faciliter l'adoption des futurs développements méthodologiques en dehors du monde académique. Pour cela, je pense que le principal levier est de renforcer les collaborations entre chercheurs et acteurs non-académiques de la conservation, ce que les précédentes étapes participeront déjà à faire. Un autre levier est de créer des structures mixtes réunissant des chercheurs et des gestionnaires d'espace naturels, comme cela existe par exemple aux États-Unis avec les *Cooperative Fish and Wildlife Research Units* (<https://www1.usgs.gov/coopunits/>). Il est bien sûr nécessaire de continuer à faire des recherches pour améliorer les méthodes de suivi, mais si

cela ne s'accompagne pas d'actions pour faire évoluer les pratiques de suivi des acteurs non-académiques, les résultats de ces recherches risquent de rester confinés au monde académique. Du point de vue de la conservation de la biodiversité, ce serait un échec.

0.8 Comptera-t-on encore des plantes dans 20 ans ?

Durant mon doctorat, j'ai travaillé sur les plans d'échantillonnage et la détection imparfaite des individus, avec pour objectif d'améliorer la précision et d'éviter le biais des estimations de taille et de tendance des populations de plantes. Les résultats de mes travaux permettent des améliorations allant dans ce sens sans qu'il ne soit nécessaire d'avoir recours à de nouvelles technologies, ce qui engendrerait des coûts supplémentaires pour acquérir le matériel et former les personnels. Les résultats de mes recherches sont applicables à budgets constants (mis à part les passages répétés nécessaires pour estimer la probabilité de détection) et avec les compétences actuelles des acteurs de la conservation en ce qui concerne la prise des données sur le terrain. Cependant, il est légitime de se demander si ces questions de recherche resteront encore longtemps d'actualité face aux récents progrès techniques que connaissent des domaines comme le machine learning (BOROWIEC et al., 2022) et l'ADN environnemental (VALENTINI et al., 2016), qui pourraient permettre d'automatiser au moins partiellement certains suivis de population. Je suis persuadé que les plans d'échantillonnage et les erreurs d'observation resteront des sujets de recherche pertinents malgré les progrès techniques à venir, et même que ceux-ci vont rendre les recherches sur ces sujets encore plus pertinentes. Tout d'abord, je pense que les suivis de population vont continuer à être mis en œuvre majoritairement par des observateurs humains pendant encore plusieurs décennies. En effet, il s'agit de tâches difficiles à automatiser (sites difficiles d'accès, habitats denses, tâches complexes à effectuer, etc.), et peu transférables entre espèces et entre études. Par exemple, un algorithme de machine learning entraîné pour détecter une espèce donnée dans un habitat donné à partir de photos ne permet généralement pas de détecter une autre espèce dans un autre habitat (WÄLDCHEN & MÄDER, 2018). Automatiser des suivis de population impliquerait également de former des personnes à l'usage de technologies complexes. Par ailleurs, l'enjeu économique des suivis est actuellement faible, et il y aurait peu de bénéfices économiques à faire dans ce domaine pour des en-

treprises voulant y investir. Tant que cette situation ne changera pas, je ne pense pas que le domaine connaîtra les investissements de recherche et développement qui seraient nécessaires pour automatiser à large échelle les suivis de population de plantes. Ces différents facteurs mèneront probablement à une période de coexistence prolongée entre les méthodes de suivi actuelles et les méthodes reposant sur de nouvelles technologies, comme cela arrive couramment entre anciennes et nouvelles technologies (ANDERSON & TUSHMAN, 1990; NAIR & AHLSTROM, 2003). A l'horizon des prochaines décennies, je pense donc qu'un certain degré d'automatisation arrivera, mais qu'il sera limité aux suivis qui s'y prêtent le plus. Par exemple, il est possible que l'occurrence d'espèces difficiles à détecter, à cause de leur discrétion ou de la difficulté à parcourir leur habitat, soit de plus en plus souvent suivie grâce à de l'ADN environnemental d'échantillons d'eau ou de sol car ce sera moins coûteux que d'utiliser des méthodes de prospection par des observateurs humains (voir par exemple ARIZA et al., 2023; SCRIVER et al., 2015).

La deuxième raison pour laquelle je pense que les plans d'échantillonnage et l'estimation des erreurs d'observation resteront des sujets de recherche d'actualité est que même si l'observateur est une machine et non un humain, il n'y aura aucun intérêt à prospector l'intégralité des zones d'étude alors qu'en observer une petite partie et extrapoler les estimations à l'ensemble de la zone d'étude permet généralement d'avoir des estimations suffisamment précises pour l'usage qui en est fait. De plus, aucune méthode de détection automatique ne pourra jamais avoir une détection parfaite en toutes circonstances et pour toutes les espèces. Les méthodes statistiques développées pour estimer les erreurs d'observation des humains serviront de base pour développer celles qui permettront d'estimer les erreurs des méthodes de détection automatique. Des recherches allant dans ce sens ont d'ailleurs déjà été amorcées (DAMGAARD, 2021; GIMENEZ et al., 2022).

0.9 De l'utilité des suivis de population dans la lutte contre la crise de la biodiversité

En dehors des questions de fiabilité des suivis de population et d'incertitude des estimations qu'ils produisent, il peut être intéressant de prendre du recul et de se questionner sur l'utilité même de l'activité de suivi. En effet, malgré le rôle crucial que jouent les suivis dans la conservation de la biodiversité, il est évident que disposer d'estimations exactes et précises des tailles et des tendances de population ne suffira pas à inverser le déclin de la biodiversité. Dans certaines situations, les suivis peuvent n'être d'aucune utilité pour la conservation, voire détourner des ressources qui auraient été plus utiles si elles avaient été consacrées à d'autres actions. En effet, réaliser des suivis coûte des ressources, d'autant plus si l'objectif de précision est élevé, puisque cela nécessite une taille d'échantillon, et donc un effort de terrain, plus élevé. Or, la conservation dispose de ressources limitées, et les actions de conservation qui permettent de secourir une population en déclin sont également coûteuses. Il est donc nécessaire de trouver un compromis entre allouer les ressources aux suivis et aux actions de conservation. Allouer une proportion trop importante des ressources aux suivis peut réduire l'efficacité des programmes de conservation (BUXTON et al., 2020). La manière de répondre à ce compromis a fait l'objet d'une relative controverse au début des années 2010 (voir notamment GEUPEL et al., 2011 ; MCDONALD-MADDEN et al., 2010, 2011). Un des arguments forts de ce débat était que si les menaces pesant sur un objectif de conservation (par exemple une population) sont connues et que l'on sait quelle est la meilleure intervention possible pour conserver cet objectif, il est conseillé d'utiliser toutes les ressources à disposition pour les mesures de conservation et déconseillé de réaliser un suivi, qui ne ferait que détourner des ressources d'un poste de dépenses plus utile (MCDONALD-MADDEN et al., 2010). Cette situation est relativement simpliste et probablement rarement rencontrée en réalité, puisqu'elle fait abstraction de toute incertitude (sur les menaces, sur l'efficacité supposée des différentes interventions possibles, sur l'efficacité réelle de l'intervention réalisée, etc.), alors que l'incertitude est inhérente à la biologie de la conservation (GEUPEL et al., 2011). Néanmoins, cela illustre que dans certaines situations, se passer totalement de suivi et allouer l'intégralité des ressources disponibles aux mesures de conservation pourrait effectivement être la meilleure déci-

sion pour la conservation. En outre, il existe effectivement des cas tragiques d'espèces qui se sont éteintes car les mesures de conservation ont été trop tardives, alors que la tendance des populations était parfaitement connue (des exemples d'espèces ainsi « *monitored to extinction* » sont présentés dans MARTIN et al., 2012).

Par ailleurs, les causes fondamentales de la crise de la biodiversité, telles que la destruction des habitats et la surexploitation des ressources naturelles, sont des conséquences du fonctionnement de nos systèmes socio-économiques actuels (IPBES, 2019). Disposer d'estimations précises et fiables des tendances de population est crucial pour déclencher des mesures de conservation, mais il serait naïf de croire qu'il s'agit de l'unique verrou empêchant de lutter efficacement contre la crise de la biodiversité. Les décisions de protéger des populations menacées et plus largement de protéger la biodiversité sont avant tout des choix politiques et de société. La conservation de la biodiversité nécessite une combinaison d'efforts pour améliorer le suivi de la biodiversité afin d'identifier les populations (ou communautés ou écosystèmes) les plus menacées et mener davantage d'actions de conservation ciblées sur ces entités. Cependant, je pense que lutter contre la crise de la biodiversité en agissant uniquement pour conserver des populations, communautés ou écosystèmes spécifiques, sans agir sur les causes fondamentales de la crise, est une approche vouée à l'échec. Conserver les mêmes systèmes socio-économiques tout en luttant contre la crise de la biodiversité mènera à une bataille perdue d'avance, où la biologie de la conservation luttera pour protéger une biodiversité soumise à des pressions croissantes (RIGAL, 2021). J'espère que nous allons amorcer ces changements avant d'y être contraints par le changement climatique, la crise de la biodiversité et l'épuisement des sources d'énergie fossile, afin d'avoir un plus large choix sur nos futurs possibles. En outre, j'espère que la biologie de la conservation jouera un rôle central dans les débats sur ce sujet en informant les citoyens sur quels modèles socio-économiques peuvent fonctionner et lesquels ne fonctionneront pas car ils ne permettent pas une conservation pérenne de la biodiversité. Autrement dit, je pense, et j'espère, que l'avenir de la biologie de la conservation sera de participer à répondre à la question suivante : *quels modèles de société sont possibles et lesquels ne peuvent pas l'être ?* Les choix qui en découleront, quant à eux, sont politiques et non scientifiques.

Références

- ALEXANDER, H. M., SLADE, N. A., & KETTLE, W. D. (1997). Application of mark-recapture models to estimation of the population size of plants. *Ecology*, 78(4), 1230-1237. [https://doi.org/10.1890/0012-9658\(1997\)078\[1230:AOMRMT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1230:AOMRMT]2.0.CO;2) (cf. p. 160)
- ANDERSON, P., & TUSHMAN, M. L. (1990). Technological Discontinuities and Dominant Designs : A Cyclical Model of Technological Change. *Administrative Science Quarterly*, 35(4), 604-633. <https://doi.org/10.2307/2393511> (cf. p. 173)
- ANDRELLO, M., NICOLE, F., TILL-BOTTRAUD, I., & GAGGIOTTI, O. E. (2012). Effect of Stage-Specific Vital Rates on Population Growth Rates and Effective Population Sizes in an Endangered Iteroparous Plant. *Conservation Biology*, 26(2), 208-217. <https://doi.org/10.1111/j.1523-1739.2011.01815.x> (cf. p. 166)
- ARIZA, M., FOUKS, B., MAUVISSEAU, Q., HALVORSEN, R., ALSOS, I. G., & de BOER, H. J. (2023). Plant biodiversity assessment through soil eDNA reflects temporal and local diversity. *Methods in Ecology and Evolution*, 14(2), 415-430. <https://doi.org/10.1111/2041-210X.13865> (cf. p. 173)
- BESBEAS, P., FREEMAN, S. N., MORGAN, B. J. T., & CATCHPOLE, E. A. (2002). Integrating Mark-Recapture-Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters. *Biometrics*, 58(3), 540-547 (cf. p. 166).
- BOROWIEC, M. L., DIKOW, R. B., FRANDBSEN, P. B., MCKEEN, A., VALENTINI, G., & WHITE, A. E. (2022). Deep learning as a tool for ecology and evolution. *Methods in Ecology and Evolution*, 13(8), 1640-1660. <https://doi.org/10.1111/2041-210X.13901> (cf. p. 172)
- BUXTON, R. T., AVERY-GOMM, S., LIN, H.-Y., SMITH, P. A., COOKE, S. J., & BENNETT, J. R. (2020). Half of resources in threatened species conservation plans are allocated to research and monitoring. *Nature Communications*, 11(1), 4668. <https://doi.org/10.1038/s41467-020-18486-6> (cf. p. 174)
- CASNER, K. L., FORISTER, M. L., RAM, K., & SHAPIRO, A. M. (2014). The utility of repeated presence data as a surrogate for counts : a case study using butterflies. *Journal of Insect Conservation*, 18(1), 13-27. <https://doi.org/10.1007/s10841-013-9610-8> (cf. p. 162)
- CHEN, G., KÉRY, M., PLATTNER, M., MA, K., & GARDNER, B. (2013). Imperfect detection is the rule rather than the exception in plant distribution studies. *Journal of Ecology*, 101(1), 183-191. <https://doi.org/10.1111/1365-2745.12021> (cf. p. 160)
- CHEN, G., KÉRY, M., ZHANG, J., & MA, K. (2009). Factors affecting detection probability in plant distribution studies. *Journal of Ecology*, 97(6), 1383-1389. <https://doi.org/10.1111/j.1365-2745.2009.01560.x> (cf. p. 161)
- DAMGAARD, C. (2021). Integrating Hierarchical Statistical Models and Machine-Learning Algorithms for Ground-Truthing Drone Images of the Vegetation : Taxonomy, Abundance and Population Ecological Models. *Remote Sensing*, 13(6), 1161. <https://doi.org/10.3390/rs13061161> (cf. p. 165, 173)
- DUCHENNE, F., PORCHER, E., MIHOUB, J.-B., LOÏS, G., & FONTAINE, C. (2022). Controversy over the decline of arthropods : a matter of temporal baseline? *Peer Community Journal*, 2. <https://doi.org/10.24072/pcjournal.131> (cf. p. 160)

- ERWIN, R. M. (1982). Observer Variability in Estimating Numbers : An Experiment. *Journal of Field Ornithology*, 53(2), 159-167 (cf. p. 162).
- FEDOROFF, E. (2009). *Observatoire de la flore de Bourgogne - Programme 2009-2019 - Méthode et Plan d'échantillonnage* (rapp. tech.). Observatoire de la flore de Bourgogne Programme 2009 - 2019 Méthode et Plan d'échantillonnage Conservatoire botanique national du Bassin parisien. (Cf. p. 169).
- FRASER, L. H., HENRY, H. A., CARLYLE, C. N., WHITE, S. R., BEIERKUHNLIN, C., CAHILL JR, J. F., CASPER, B. B., CLELAND, E., COLLINS, S. L., DUKES, J. S., KNAPP, A. K., LIND, E., LONG, R., LUO, Y., REICH, P. B., SMITH, M. D., STERNBERG, M., & TURKINGTON, R. (2013). Coordinated distributed experiments : an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment*, 11(3), 147-155. <https://doi.org/10.1890/110279> (cf. p. 163)
- FRECKLETON, R. P., GILL, J. A., NOBLE, D., & WATKINSON, A. R. (2005). Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. *Journal of Animal Ecology*, 74(2), 353-364. <https://doi.org/10.1111/j.1365-2656.2005.00931.x> (cf. p. 163)
- FRÉVILLE, H., CHOQUET, R., PRADEL, R., & CHEPTOU, P.-O. (2013). Inferring seed bank from hidden Markov models : new insights into metapopulation dynamics in plants. *Journal of Ecology*, 101(6), 1572-1580. <https://doi.org/10.1111/1365-2745.12141> (cf. p. 165)
- GÄRLING, T., & GOLLEDGE, R. G. (1989). Environmental Perception and Cognition. In E. H. ZUBE & G. T. MOORE (Éd.), *Advance in Environment, Behavior, and Design : Volume 2* (p. 203-236). Springer US. https://doi.org/10.1007/978-1-4613-0717-4_7. (Cf. p. 164)
- GARRARD, G. E., BEKESY, S. A., MCCARTHY, M. A., & WINTLE, B. A. (2008). When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology*, 33(8), 986-998. <https://doi.org/10.1111/j.1442-9993.2008.01869.x> (cf. p. 160)
- GAZAIX, A., KLESCZEWSKI, M., BOUCHET, M.-A., CARTEREAU, M., MOLINA, J., MICHAUD, H., MULLER, S. D., PIRSOUL, L., GAUTHIER, P., GRILLAS, P., & THOMPSON, J. D. (2020). A history of discoveries and disappearances of the rare annual plant *Lythrum thesioides* M.Bieb. : new insights into its ecology and biology. *Botany Letters*, 167(2), 201-211. <https://doi.org/10.1080/23818107.2019.1684358> (cf. p. 165)
- GEUPEL, G. R., HUMPLE, D., & ROBERTS, L. J. (2011). Monitoring decisions : not as simple as they seem? *Trends in Ecology & Evolution*, 26(3), 107. <https://doi.org/10.1016/j.tree.2010.11.007> (cf. p. 174)
- GIMENEZ, O., KERVELLEC, M., FANJUL, J.-B., CHAINE, A., MARESCOT, L., BOLLET, Y., & DUCHAMP, C. (2022). Trade-off between deep learning for species identification and inference about predator-prey co-occurrence. *Computo* (cf. p. 173).
- HAUSER, C. E., GILJOHANN, K. M., MCCARTHY, M. A., GARRARD, G. E., ROBINSON, A. P., WILLIAMS, N. S. G., & MOORE, J. L. (2022). A field experiment characterizing variable detection rates during plant surveys. *Conservation Biology*, 36(3), e13888. <https://doi.org/10.1111/cobi.13888> (cf. p. 161)
- IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (rapp. tech.). Zenodo. <https://doi.org/10.5281/zenodo.6417333>. (Cf. p. 175)

- IUCN. (2019). Guidelines for Using the IUCN Red List Categories and Criteria - Version 14. (Cf. p. 163).
- JAILLOUX, A. (2010). *Les suivis dans les parcs nationaux français, une contribution originale pour l'évaluation de la biodiversité ?* (Rapp. tech.). (Cf. p. 168).
- KELLNER, K. F., & SWIHART, R. K. (2014). Accounting for Imperfect Detection in Ecology : A Quantitative Review. *Plos One*, 9(10), e111436. <https://doi.org/10.1371/journal.pone.0111436> (cf. p. 167, 170)
- KÉRY, M., GREGG, K. B., & SCHAUB, M. (2005). Demographic estimation methods for plants with unobservable life-states. *Oikos*, 108(2), 307-320. <https://doi.org/10.1111/j.0030-1299.2005.13589.x> (cf. p. 161)
- KOSHKINA, V., WANG, Y., GORDON, A., DORAZIO, R. M., WHITE, M., & STONE, L. (2017). Integrated species distribution models : combining presence-background data and site-occupancy data with imperfect detection. *Methods in Ecology and Evolution*, 8(4), 420-430. <https://doi.org/10.1111/2041-210X.12738> (cf. p. 166)
- LARA-ROMERO, C., CRUZ, M. d. I., ESCRIBANO-ÁVILA, G., GARCÍA-FERNÁNDEZ, A., & IRIONDO, J. M. (2016). What causes conspecific plant aggregation ? Disentangling the role of dispersal, habitat heterogeneity and plant-plant interactions. *Oikos*, 125(9), 1304-1313. <https://doi.org/https://doi.org/10.1111/oik.03099> (cf. p. 159)
- LARK, R. M., & CORSTANJE, R. (2009). Non-homogeneity of variance components from spatially nested sampling of the soil. *European Journal of Soil Science*, 60(3), 443-452. <https://doi.org/10.1111/j.1365-2389.2009.01133.x> (cf. p. 159)
- LE COZ, S., CHEPTOU, P.-O., & PEYRARD, N. (2019). A spatial Markovian framework for estimating regional and local dynamics of annual plants with dormancy. *Theoretical Population Biology*, 127, 120-132. <https://doi.org/10.1016/j.tpb.2019.03.002> (cf. p. 165)
- LENOIR, J., GEGOUT, J. C., MARQUET, P. A., de RUFFRAY, P., & BRISSE, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768-1771. <https://doi.org/10.1126/science.1156831> (cf. p. 159)
- MARSH, D. M., & TRENHAM, P. C. (2008). Current Trends in Plant and Animal Population Monitoring. *Conservation Biology*, 22(3), 647-655. <https://doi.org/10.1111/j.1523-1739.2008.00927.x> (cf. p. 168, 170)
- MARTIN, T. G., NALLY, S., BURBIDGE, A. A., ARNALL, S., GARNETT, S. T., HAYWARD, M. W., LUMSDEN, L. F., MENKHORST, P., McDONALD-MADDEN, E., & POSSINGHAM, H. P. (2012). Acting fast helps avoid extinction. *Conservation Letters*, 5(4), 274-280. <https://doi.org/10.1111/j.1755-263X.2012.00239.x> (cf. p. 175)
- MCDONALD-MADDEN, E., BAXTER, P. W. J., FULLER, R. A., MARTIN, T. G., GAME, E. T., MONTAMBAULT, J., & POSSINGHAM, H. P. (2010). Monitoring does not always count. *Trends in Ecology & Evolution*, 25(10), 547-550. <https://doi.org/10.1016/j.tree.2010.07.002> (cf. p. 174)
- MCDONALD-MADDEN, E., BAXTER, P. W. J., FULLER, R. A., MARTIN, T. G., GAME, E. T., MONTAMBAULT, J., & POSSINGHAM, H. P. (2011). Should we implement monitoring or research for conservation ? *Trends in Ecology & Evolution*, 26(3), 108-109. <https://doi.org/10.1016/j.tree.2010.12.005> (cf. p. 174)
- NAIR, A., & AHLSTROM, D. (2003). Delayed creative destruction and the coexistence of technologies. *Journal of Engineering and Technology Management*, 20(4), 345-365. <https://doi.org/10.1016/j.jengtecman.2003.08.003> (cf. p. 173)

- NOON, B. R., BAILEY, L. L., SISK, T. D., & MCKELVEY, K. S. (2012). Efficient Species-Level Monitoring at the Landscape Scale. *Conservation Biology*, 26(3), 432-441. <https://doi.org/10.1111/j.1523-1739.2012.01855.x> (cf. p. 162)
- PLUNTZ, M., LE COZ, S., PEYRARD, N., PRADEL, R., CHOQUET, R., & CHEPTOU, P.-O. (2018). A general method for estimating seed dormancy and colonisation in annual plants from the observation of existing flora. *Ecology Letters*, 21(9), 1311-1318. <https://doi.org/10.1111/ele.13097> (cf. p. 165)
- QUÉROUÉ, M., BARBRAUD, C., BARRAQUAND, F., TUREK, D., DELORD, K., PACOUREAU, N., & GIMENEZ, O. (2021). Multispecies integrated population model reveals bottom-up dynamics in a seabird predator-prey system. *Ecological Monographs*, 91(3), e01459. <https://doi.org/10.1002/ecm.1459> (cf. p. 166)
- RIGAL, S. (2021). "Tout est lié" : réponses complexes de la biodiversité aux changements globaux et déterminants socio-économiques (These de doctorat). Montpellier. (Cf. p. 175).
- RIGAL, S., DEVICTOR, V., & DAKOS, V. (2020). A method for classifying and comparing non-linear trajectories of ecological variables. *Ecological Indicators*, 112, 106113. <https://doi.org/10.1016/j.ecolind.2020.106113> (cf. p. 160)
- ROMINGER, K. R., DENITTIS, A., & MEYER, S. E. (2021). Using drone imagery analysis in rare plant demographic studies. *Journal for Nature Conservation*, 62, 126020. <https://doi.org/10.1016/j.jnc.2021.126020> (cf. p. 164)
- ROYLE, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, 60(1), 108-115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x> (cf. p. 161)
- SCHAUB, M., & ABADI, F. (2011). Integrated population models : a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, 152(1), 227-237. <https://doi.org/10.1007/s10336-010-0632-7> (cf. p. 166)
- SCRIVER, M., MARINICH, A., WILSON, C., & FREELAND, J. (2015). Development of species-specific environmental DNA (eDNA) markers for invasive aquatic plants. *Aquatic Botany*, 122, 27-31. <https://doi.org/10.1016/j.aquabot.2015.01.003> (cf. p. 173)
- SEABLOOM, E. W., BJORNSTAD, O. N., BOLKER, B. M., & REICHMAN, O. J. (2005). Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecological Monographs*, 75(2), 199-214. <https://doi.org/10.1890/03-0841> (cf. p. 159)
- SHACKLETON, R. T., PETITPIERRE, B., PAJKOVIC, M., DESSIMOZ, F., BRÖNNIMANN, O., CATTIN, L., ČEJKOVÁ, Š., KULL, C. A., PERGL, J., PYŠEK, P., YOCCOZ, N., & GUISAN, A. (2020). Integrated Methods for Monitoring the Invasive Potential and Management of *Heracleum mantegazzianum* (giant hogweed) in Switzerland. *Environmental Management*, 65(6), 829-842. <https://doi.org/10.1007/s00267-020-01282-9> (cf. p. 158)
- STREBEL, N., FISS, C. J., KELLNER, K. F., LARKIN, J. L., KÉRY, M., & COHEN, J. (2021). Estimating abundance based on time-to-detection data. *Methods in Ecology and Evolution*, n/a(n/a). <https://doi.org/10.1111/2041-210X.13570> (cf. p. 161)
- TEMPEL, D. J., & GUTIERREZ, R. J. (2013). Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl. *Conservation Biology*, 27(5), 1087-1095. <https://doi.org/10.1111/cobi.12074> (cf. p. 162)

- THOMPSON, K., & GRIME, J. P. (1979). Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats. *Journal of Ecology*, 67(3), 893-921. <https://doi.org/10.2307/2259220> (cf. p. 165)
- THOMPSON, K., BAKKER, J. P., & BEKKER, R. M. (1997). *The Soil Seed Banks of North West Europe : Methodology, Density and Longevity*. Cambridge University Press. (Cf. p. 165).
- THOMPSON, S. (1990). Adaptive Cluster Sampling. *Journal of the American Statistical Association*, 85(412), 1050-1059. <https://doi.org/10.2307/2289601> (cf. p. 158)
- TURK, P., & BORKOWSKI, J. J. (2005). A review of adaptive cluster sampling : 1990–2003. *Environmental and Ecological Statistics*, 12(1), 55-94. <https://doi.org/10.1007/s10651-005-6818-0> (cf. p. 158)
- URQUHART, N. S. (2012). The role of monitoring design in detecting trend in long-term ecological monitoring studies. In A. B. COOPER, D. S. LICHT, J. J. MILLSPAUGH & R. A. GITZEN (Éd.), *Design and Analysis of Long-term Ecological Monitoring Studies* (p. 151-173). Cambridge University Press. <https://doi.org/10.1017/CBO9781139022422.011>. (Cf. p. 159)
- VALENTINI, A., TABERLET, P., MIAUD, C., CIVADE, R., HERDER, J., THOMSEN, P. F., BELLEMAIN, E., BESNARD, A., COISSAC, E., BOYER, F., GABORIAUD, C., JEAN, P., POULET, N., ROSET, N., COPP, G. H., GENIEZ, P., PONT, D., ARGILLIER, C., BAUDOIN, J.-M., ... DEJEAN, T. (2016). Next-generation monitoring of aquatic biodiversity using environmental DNA metabarcoding. *Molecular Ecology*, 25(4), 929-942. <https://doi.org/10.1111/mec.13428> (cf. p. 172)
- VITASSE, Y., URSENBACHER, S., KLEIN, G., BOHNENSTENGEL, T., CHITTARO, Y., DELESTRADE, A., MONNERAT, C., REBETEZ, M., RIXEN, C., STREBEL, N., SCHMIDT, B. R., WIPF, S., WOHLGEMUTH, T., YOCCOZ, N. G., & LENOIR, J. (2021). Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews*, 96(5), 1816-1835. <https://doi.org/10.1111/brv.12727> (cf. p. 159)
- WÄLDCHEN, J., & MÄDER, P. (2018). Machine learning for image based species identification. *Methods in Ecology and Evolution*, 9(11), 2216-2225. <https://doi.org/10.1111/2041-210X.13075> (cf. p. 172)
- WEBSTER, R., WELHAM, S. J., POTTS, J. M., & OLIVER, M. A. (2006). Estimating the spatial scales of regionalized variables by nested sampling, hierarchical analysis of variance and residual maximum likelihood. *Computers & Geosciences*, 32(9), 1320-1333. <https://doi.org/10.1016/j.cageo.2005.12.002> (cf. p. 159)
- WRIGHT, W. J., IRVINE, K. M., WARREN, J. M., & BARNETT, J. K. (2017). Statistical design and analysis for plant cover studies with multiple sources of observation errors. *Methods in Ecology and Evolution*, 8(12), 1832-1841. <https://doi.org/https://doi.org/10.1111/2041-210X.12825> (cf. p. 160)
- XIROCOSTAS, Z. A., DEBONO, S. A., SLAVICH, E., & MOLES, A. T. (2022). The ZAX Herbivory Trainer—Free software for training researchers to visually estimate leaf damage. *Methods in Ecology and Evolution*, 13(3), 596-602. <https://doi.org/10.1111/2041-210X.13785> (cf. p. 162)
- ZIPKIN, E. F., & SAUNDERS, S. P. (2018). Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation*, 217, 240-250. <https://doi.org/10.1016/j.biocon.2017.10.017> (cf. p. 166)

A | Matériel supplémentaire du Chapitre 1

Supplementary material for “Monitoring plant populations : frontiers of current knowledge and methodological challenges ahead”

Appendix 1 : Detailed material and methods for Box 1 (Cross-taxa history of statistical methods used to model imperfect detection)

For five statistical models for estimating detection probability, we searched several online databases (e.g. Web of Science, Google scholar, the official websites of journals, distancesampling.org) for the first five articles using these methods for seven taxa : plants, mammals, birds, reptiles, amphibians, fishes and arthropods. The publication of these articles was represented on a timeline divided by method and taxa.

For each statistical model, a "founding" publication was identified based on various criteria detailed below. Articles prior to this publication were not accounted for. Later articles using more complex models than those developed in the founding publication take into account.

All possible names were searched for models that had several names over time (see table below). Books and technical reports were not accounted for. Proceedings papers were accounted for, but as they are often less well referenced in online databases than journal articles, we may have missed some. Only studies on populations were considered, and applications of the statistical models on communities were not considered. Statistical papers were considered if they presented an application on one of the taxa of interest using real data and presented a numerical result (e.g. just reporting that the method was tested on a dataset and did not work does not count).

Distance sampling

Founding publication : Burnham, K., Anderson, D., 1976. Mathematical-Models for Nonparametric Inferences from Line Transect Data. Biometrics 32, 325-336. <https://doi.org/10.2307/2529501>

Justification : In the chapter ‘History of Methods’ (pages 25-26) of the first book on

distance sampling, Buckland et al. (1993) say that it was the mathematical formulation of the distance sampling model given in this article that triggered all the theoretical developments that followed.

Additional information :

- We have searched WOS for all papers that cite the seminal paper and all those that mention any possible names for this method. In addition, the bibliography of distancesampling.org was studied in parallel with the corpus constituted on WOS.
- We took into account the transect sampling point method.
- We considered articles using "trapping web design" (Anderson et al. 1983), although this mixes distance sampling and removal sampling elements. Indeed, the decline in the number of individuals captured with a mark as a function of distance from the centre of the web allows the detection function to be modelled and thus the density of individuals to be estimated.
- We did not consider the articles in "Wildlife Monographs" because we could not access to their full text, and because they are more like books than articles (some are over 200 pages long).

Closed population Capture-Recapture

Founding publication : Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs* 3-135.

Justification : It's the first synthesis available to biologists of statistical developments in closed population CR models. In addition, the notation of the models presented in this article is still used today, and it was the first article to introduce the CAPTURE software, which enabled biologists without advanced mathematical training to use these models.

Additional information :

- We have considered all papers that assume that the study population is closed.
- We have accounted for methods that involve the removal of captured individuals, known as "removal sampling". Although the removal of individuals is an important difference, we have chosen to consider the removal model as a special

case of CR models, close to the Mb model presented by Otis et al. For a detailed discussion along these lines, see Rivera and McCrea (2021).

- In the years 1978-1982, some papers estimated population size by doing a linear regression on the number of individuals recaptured on successive occasions. We have not taken these papers into account.
- We have considered papers that estimate the abundance of a genus or family of insects (i.e. they can only go so far in identification, so they group all individuals of the same genus or family).
- For amphibians, we counted two papers that use models prior to Otis et al. (1978) because they are closed population CR models even if a bit archaic.

Detection/Non-Detection site occupancy

Founding publications :

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248-2255. <https://doi.org/10.2307/3072056>

Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K., Possingham, H.P., 2003. Improving Precision and Reducing Bias in Biological Surveys : Estimating False-Negative Error Rates. *Ecological Applications* 13, 1790-1801. <https://doi.org/10.1890/02-5078>

Justification : The two publications above have independently developed the same model.

Additional information :

- We have considered indiscriminately papers that cite MacKenzie et al. (2002) and Tyre et al. (2003), as it is the same model despite minor differences in formulation.

N-mixture

Founding publication : Royle, J.A., 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* 60, 108-115. <https://doi>

[.org/10.1111/j.0006-341X.2004.00142.x](https://doi.org/10.1111/j.0006-341X.2004.00142.x)

Justification : It's the first publication presenting this model.

Additional information :

- We have not considered papers that use the Royle-Nichols (2003) model.
- We have considered models with removal counts for fish. These papers model the number of individuals in successive counts by subtracting the number of individuals taken on previous occasions. This ensures that individuals are not counted several times without needing to be marked.

Time-to-detection occupancy

Founding publication : Garrard, G.E., Bekessy, S.A., McCarthy, M.A., Wintle, B.A., 2008. When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. Austral Ecol. 33, 986-998. <https://doi.org/10.1111/j.1442-9993.2008.01869.x>

Justification : It's the first publication to present this model.

Additional information :

- We only considered models that estimate occupancy as in Garrard et al. (2008). Articles that estimate numbers of individuals from time-to-detection of several individuals were not considered.

**Appendix 2 : Description of the corpus of articles used for Box 2
(Profile of plant population monitoring studies published between
2010 and 2019)**

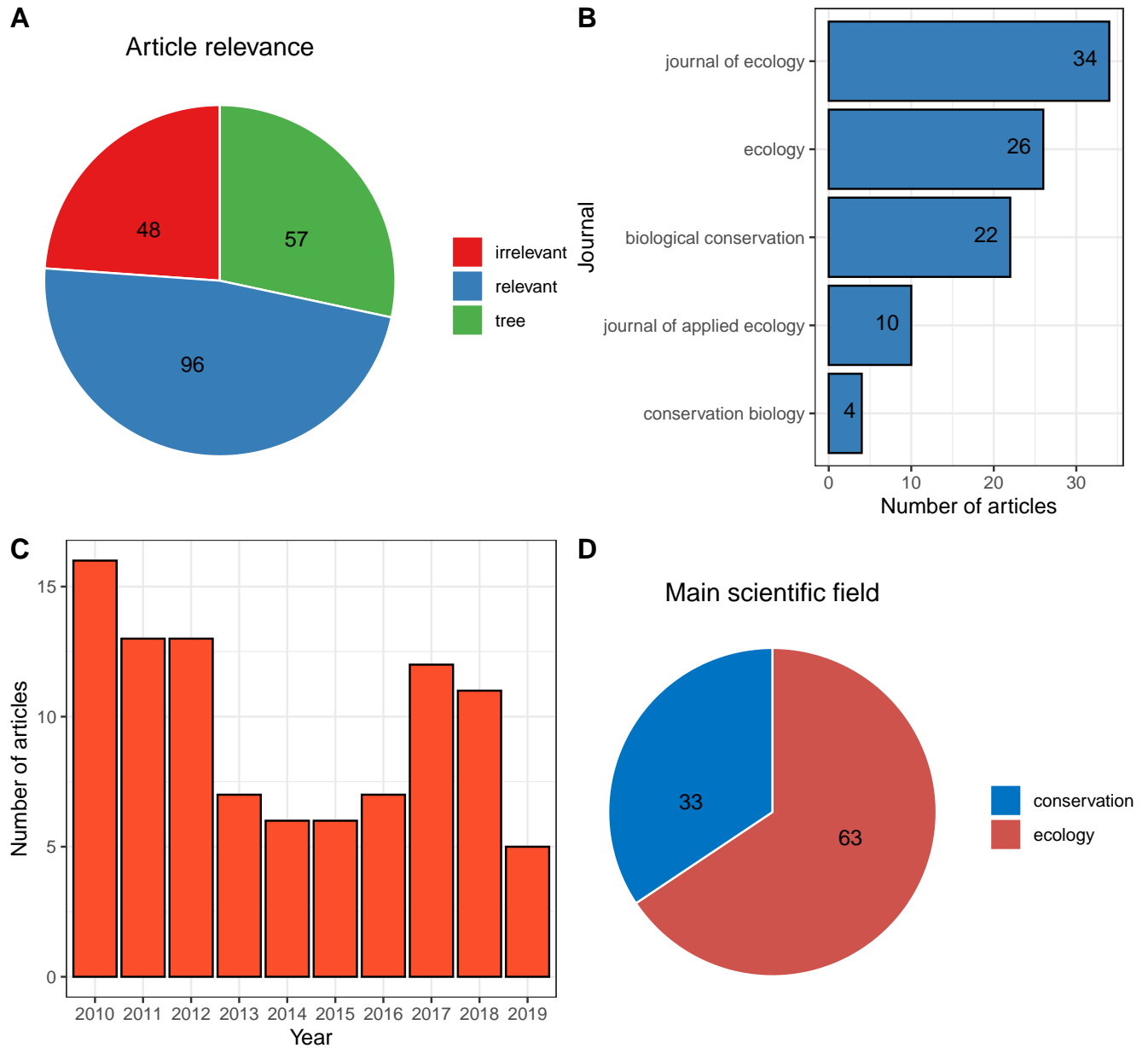


FIGURE A.1 – Description of the corpus of articles we analysed. (A) Proportion of relevant articles, irrelevant articles and articles removed from the corpus because the studied species was a tree. The following graphs refer only to the relevant articles. (B) Number of articles per journal among the relevant articles. (C) Number of articles per year. (D) Main scientific field of the articles.

B | Matériel supplémentaire du Chapitre 2

Supplementary Material for “Spatially balanced sampling methods are always more precise than random ones for estimating the size of aggregated populations”

Jan Perret, Anne Charpentier, Roger Pradel, Guillaume Papuga, Aurélien Besnard

Created on the 2022-08-01

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Appendix S1. Comparison of the three modalities used to increase the density of the virtual populations simulated with the Matérn Cluster process

Parameter values of the Matérn cluster process

Figure S1.1 shows the values of the three parameters of the Matérn cluster process we used to simulate the virtual populations in order to obtain the desired dispersion index levels. For modalities 1 and 3, we had to increase the cluster radius when increasing population density in order to maintain the same value of dispersion index. Thus, populations with the same dispersion index had larger clusters as density increased. In contrast, for modality 2, clusters had the same radius for the same level of dispersion index at all densities.

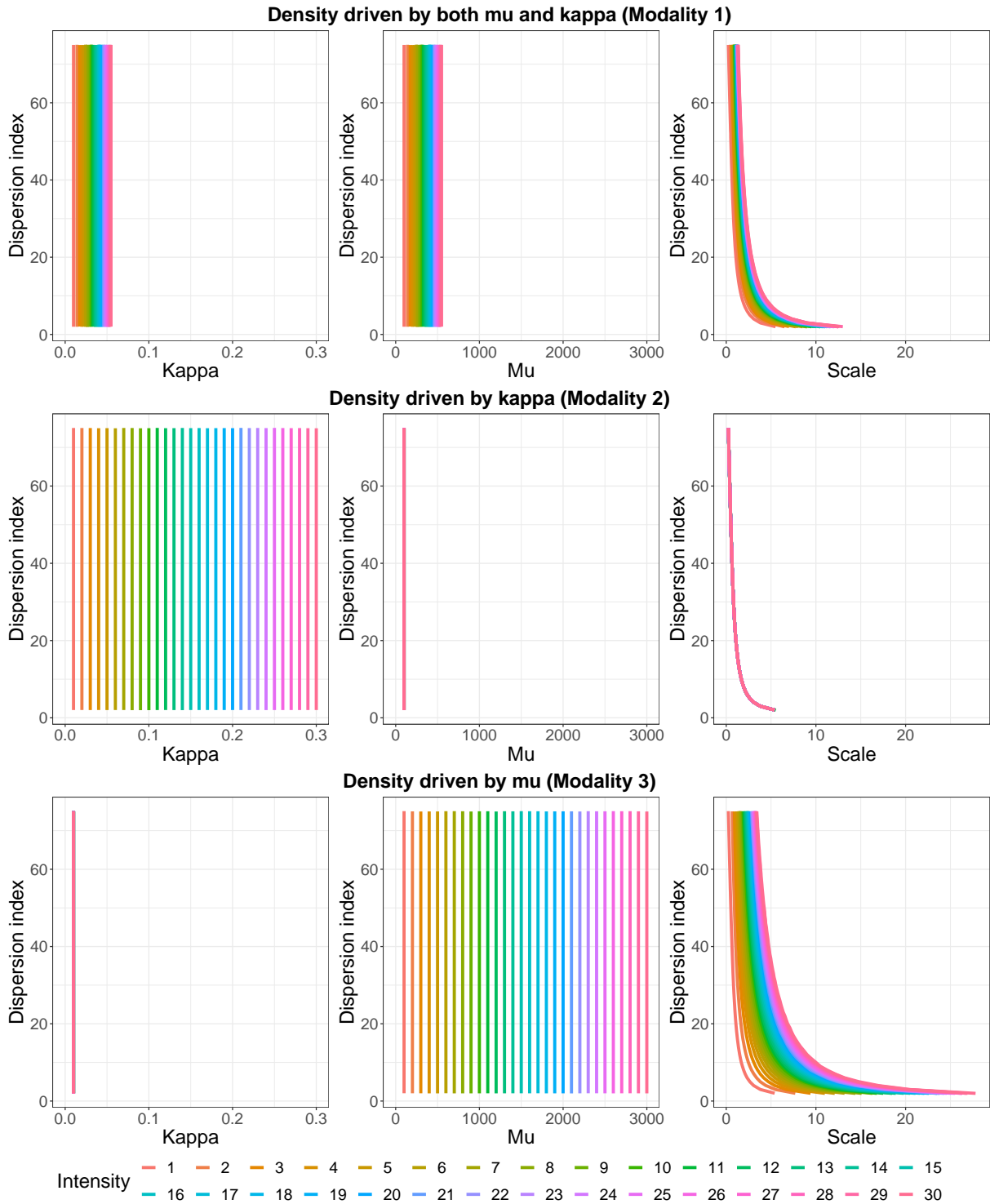
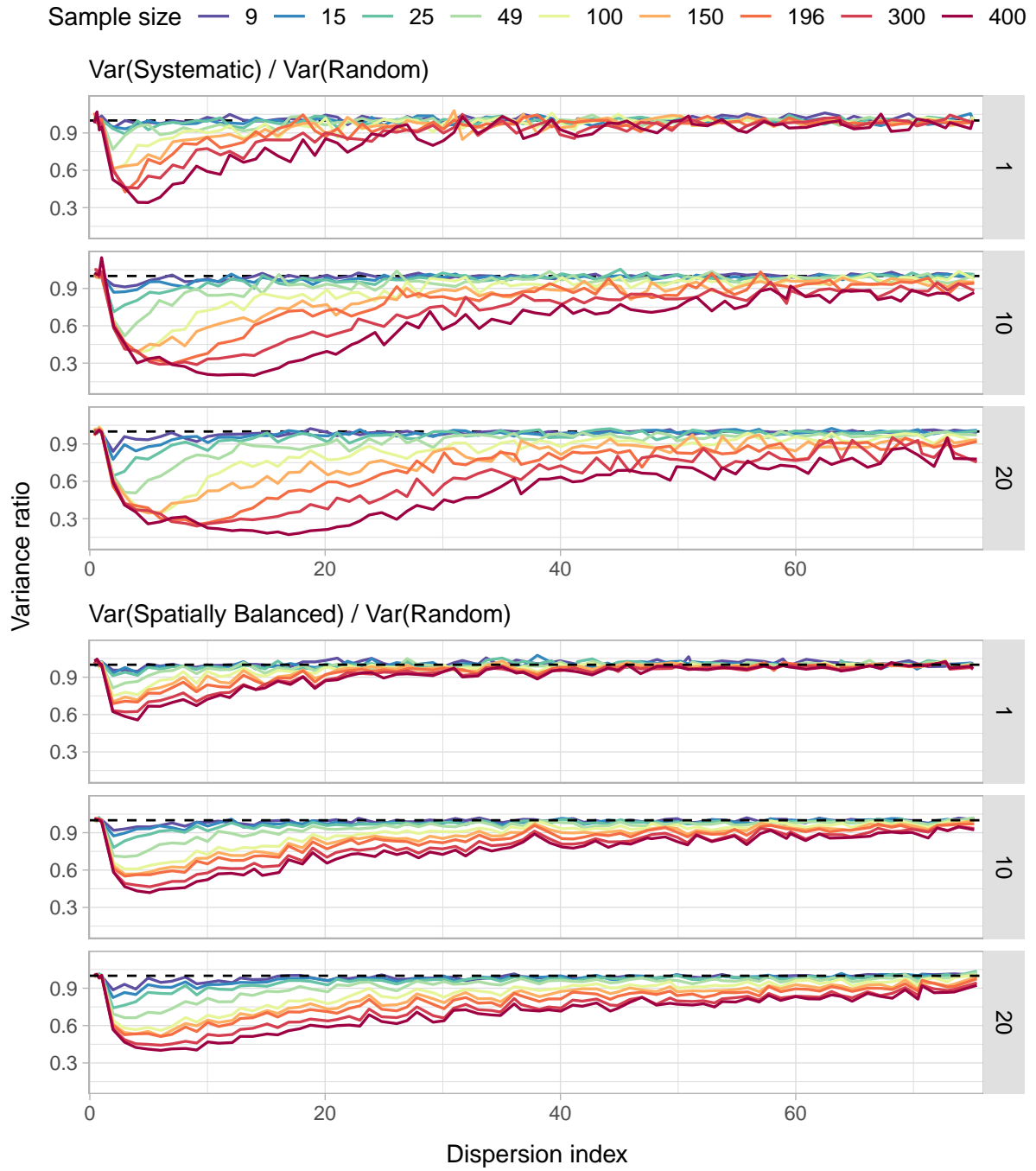


Figure S1.1: Parameter values of the Matérn cluster process used to obtain the desired dispersion index levels under the three possible modalities for increasing the mean density of the virtual populations. The three parameters were the mean density of clusters (κ), the mean number of individuals per cluster (μ), and the cluster radius (scale).

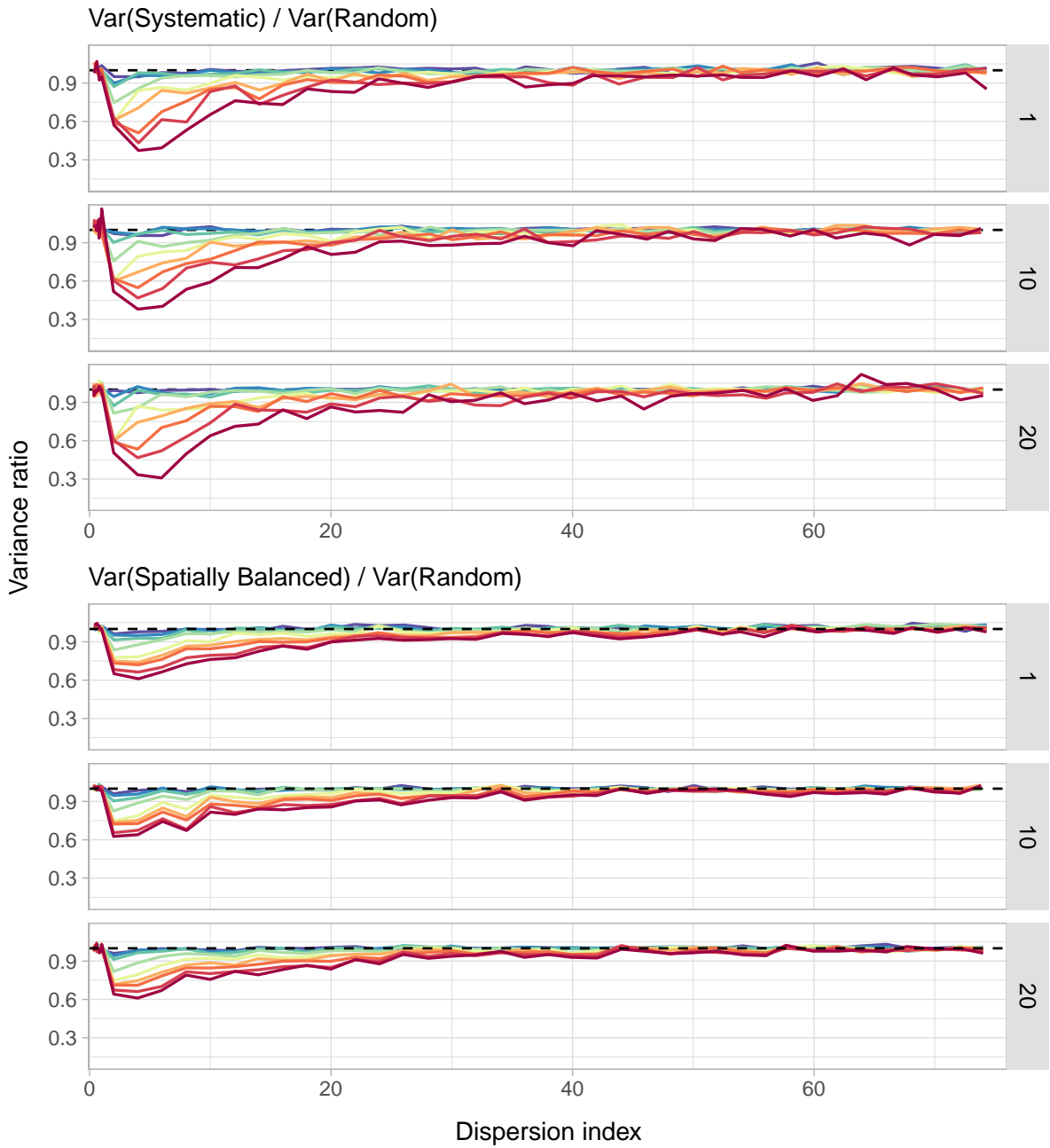
Variance ratio as a function of the dispersion index

Modality 1



Modality 2

Sample size — 9 — 15 — 25 — 49 — 100 — 150 — 196 — 300 — 400



Modality 3

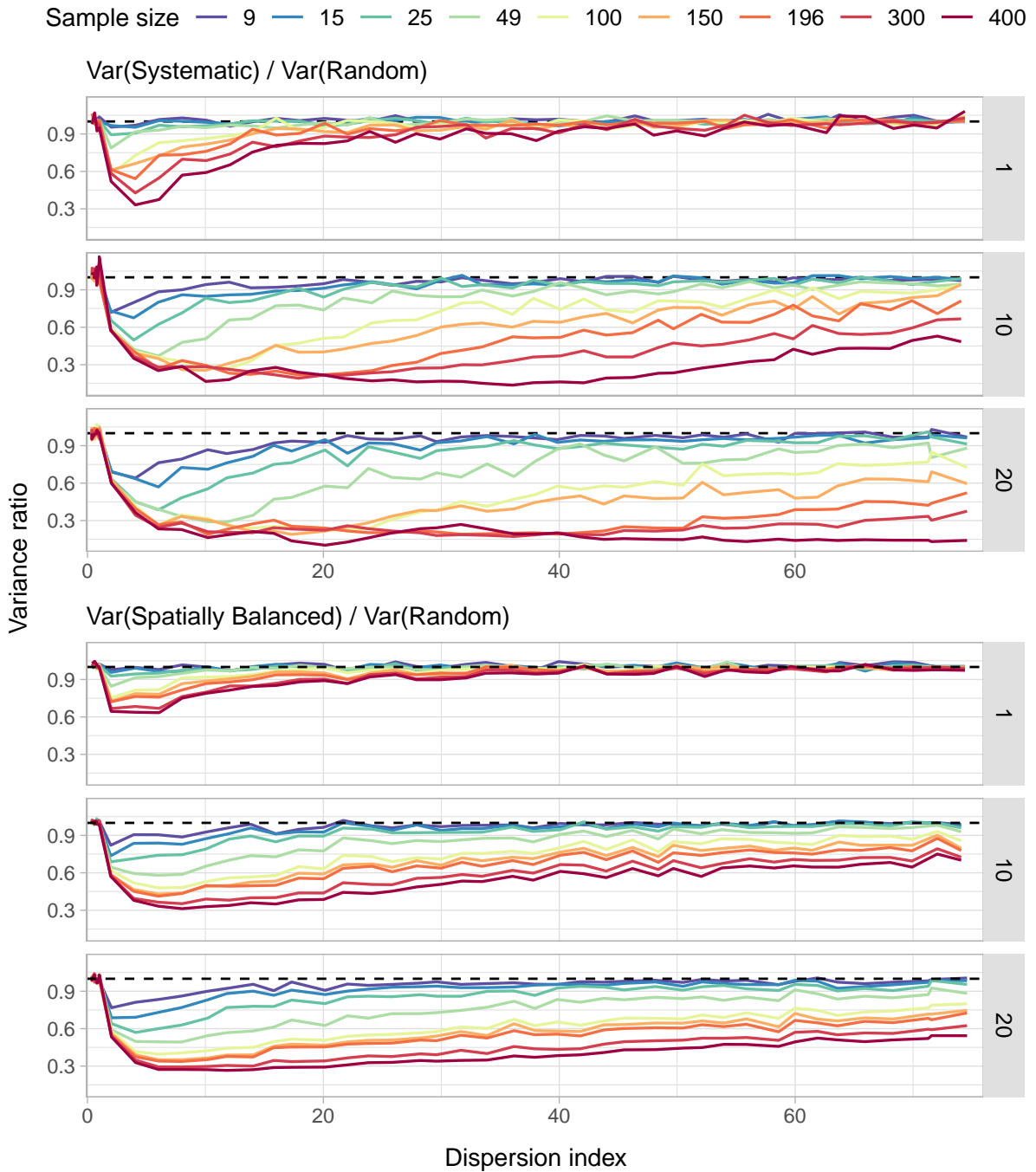
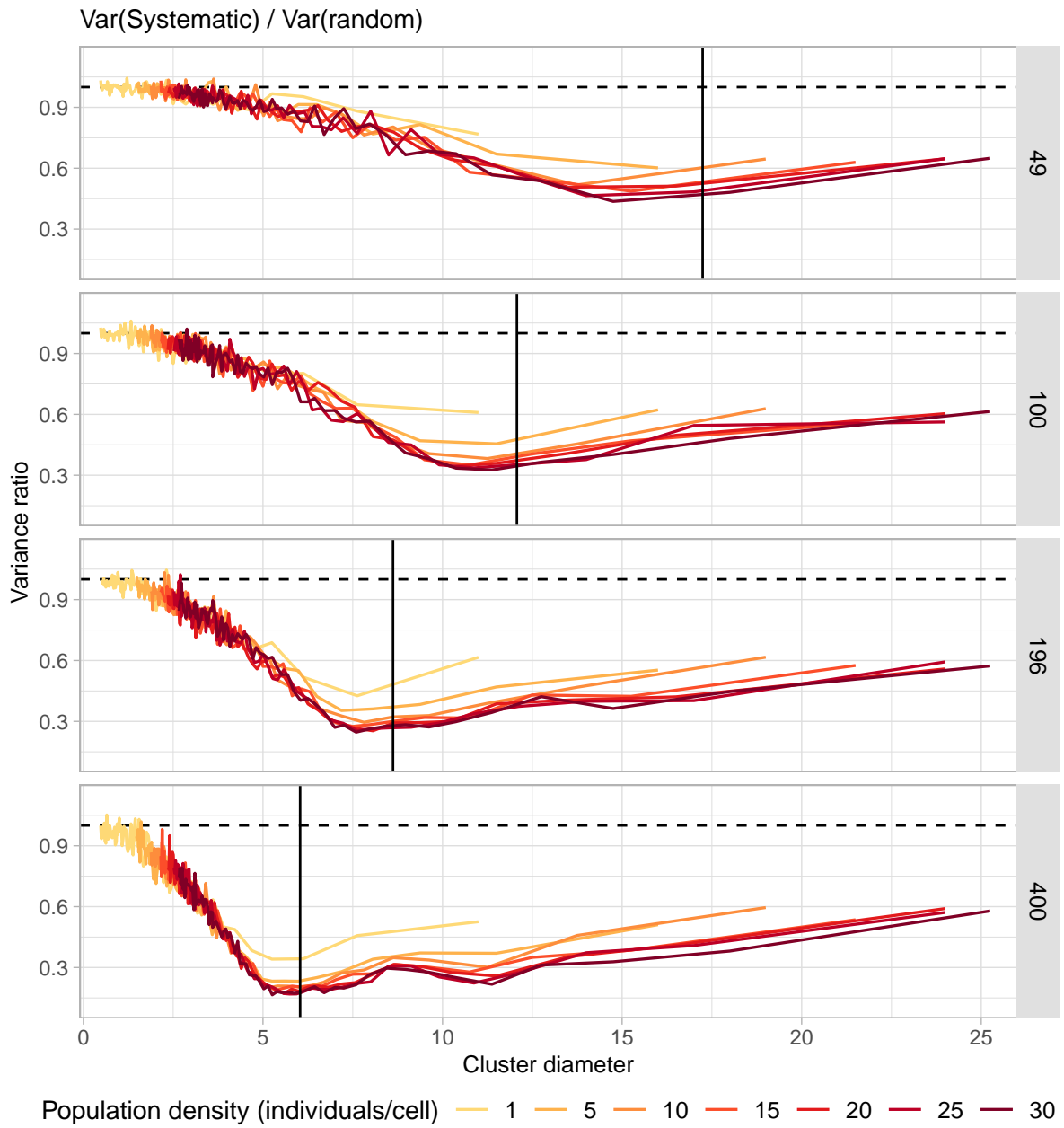


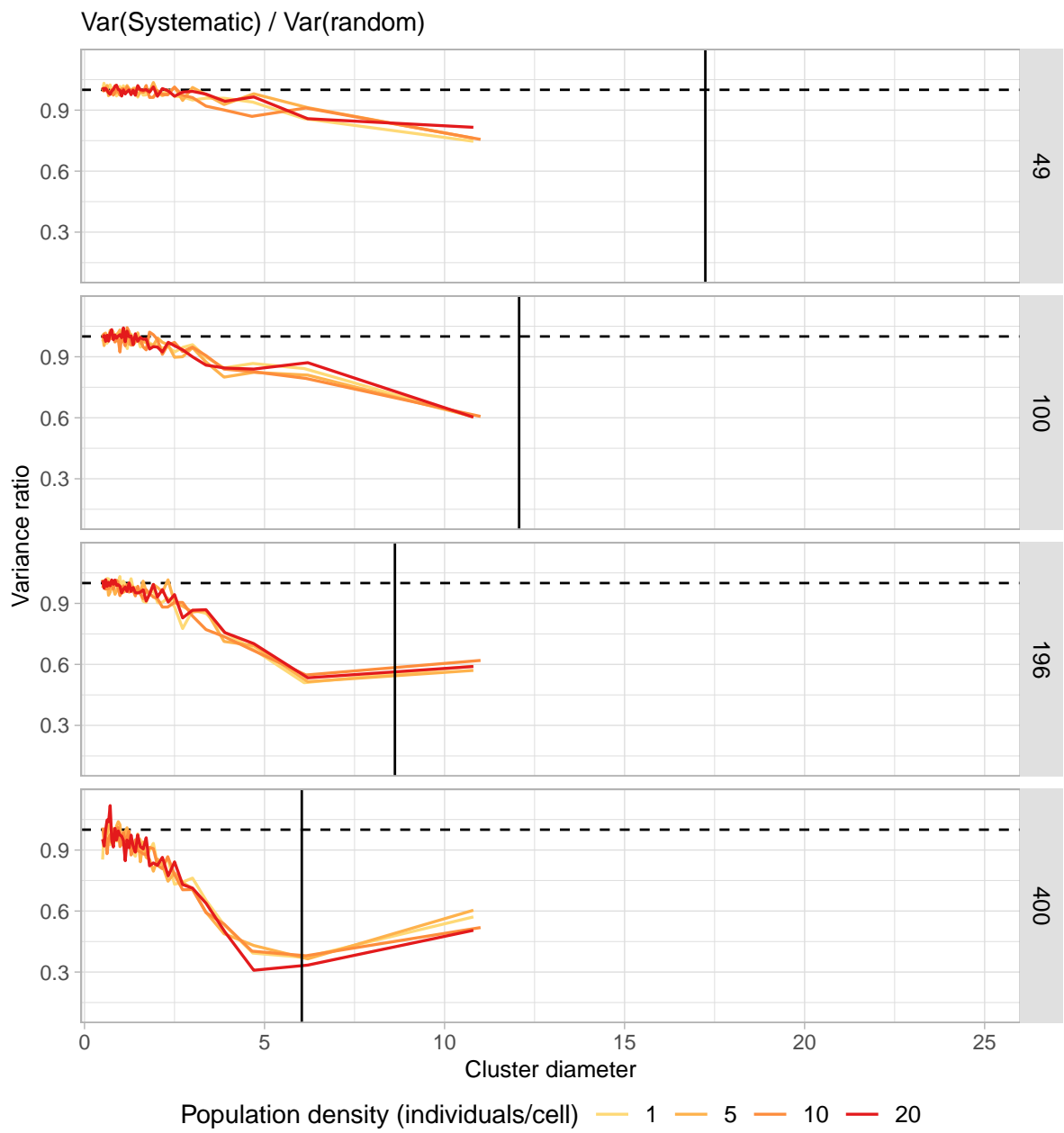
Figure S1.2: Ratio of the sampling variance of systematic sampling (SYS) and spatially balanced sampling (SBS) over the sampling variance of simple random sampling (SRS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell). For the aggregated populations, density was increased by increasing either both kappa and mu (modality 1), only kappa (modality 2) or only mu (modality 3). Each point of the curves is the ratio of two sampling variances estimated from 1,000 samples drawn for 60 populations.

SYS variance ratio as a function of cluster diameter

Modality 1



Modality 2



Modality 3

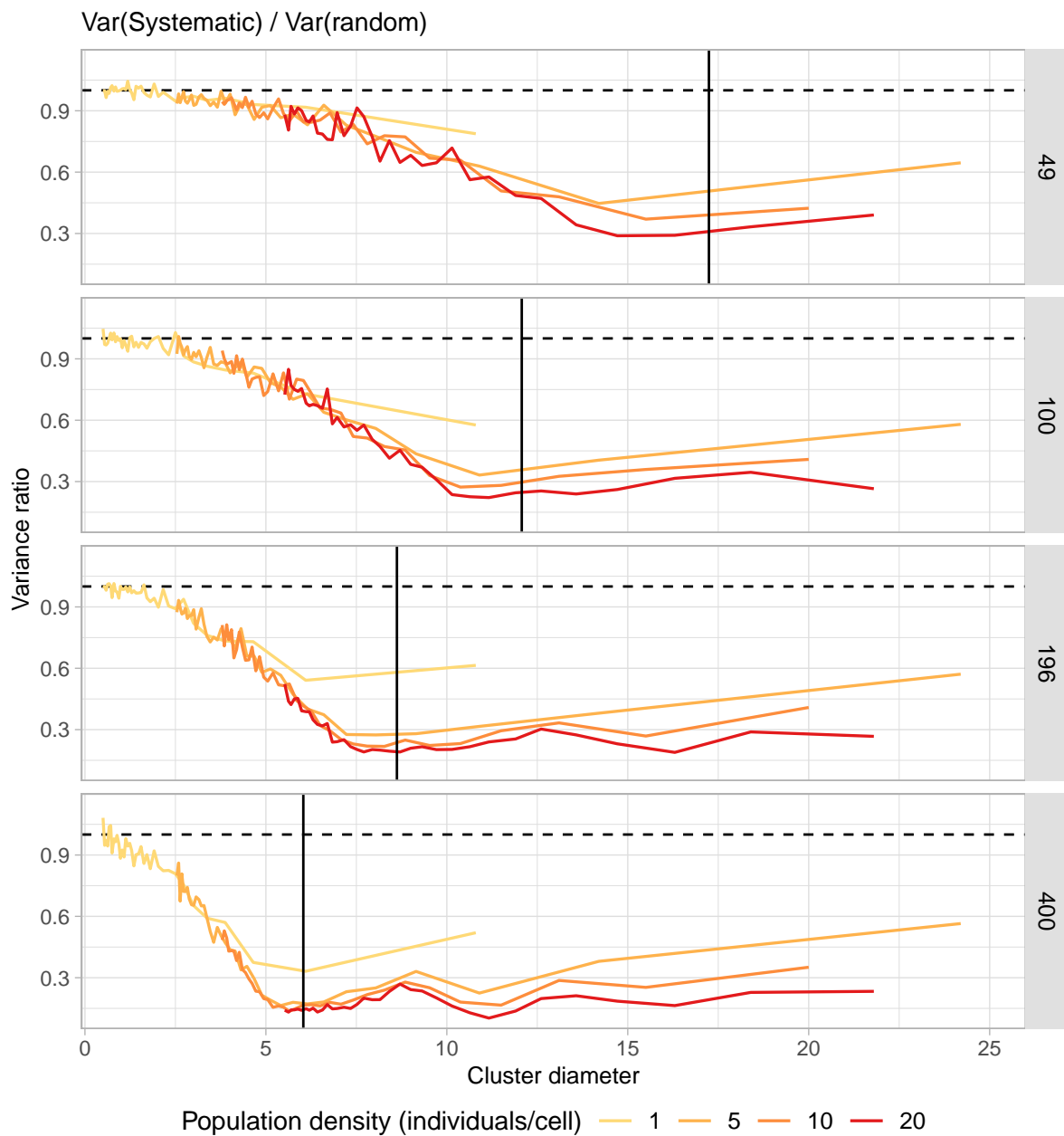
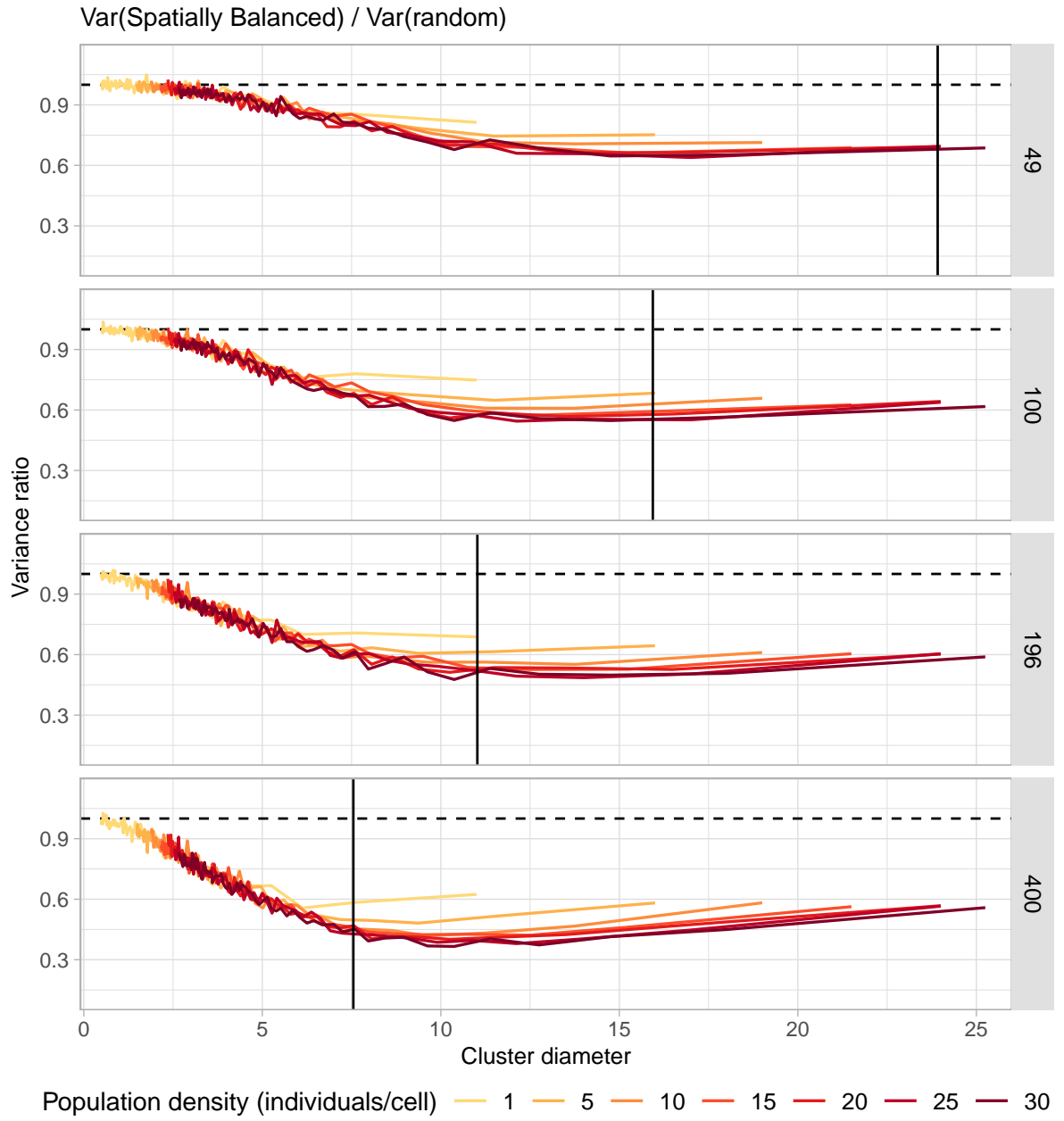


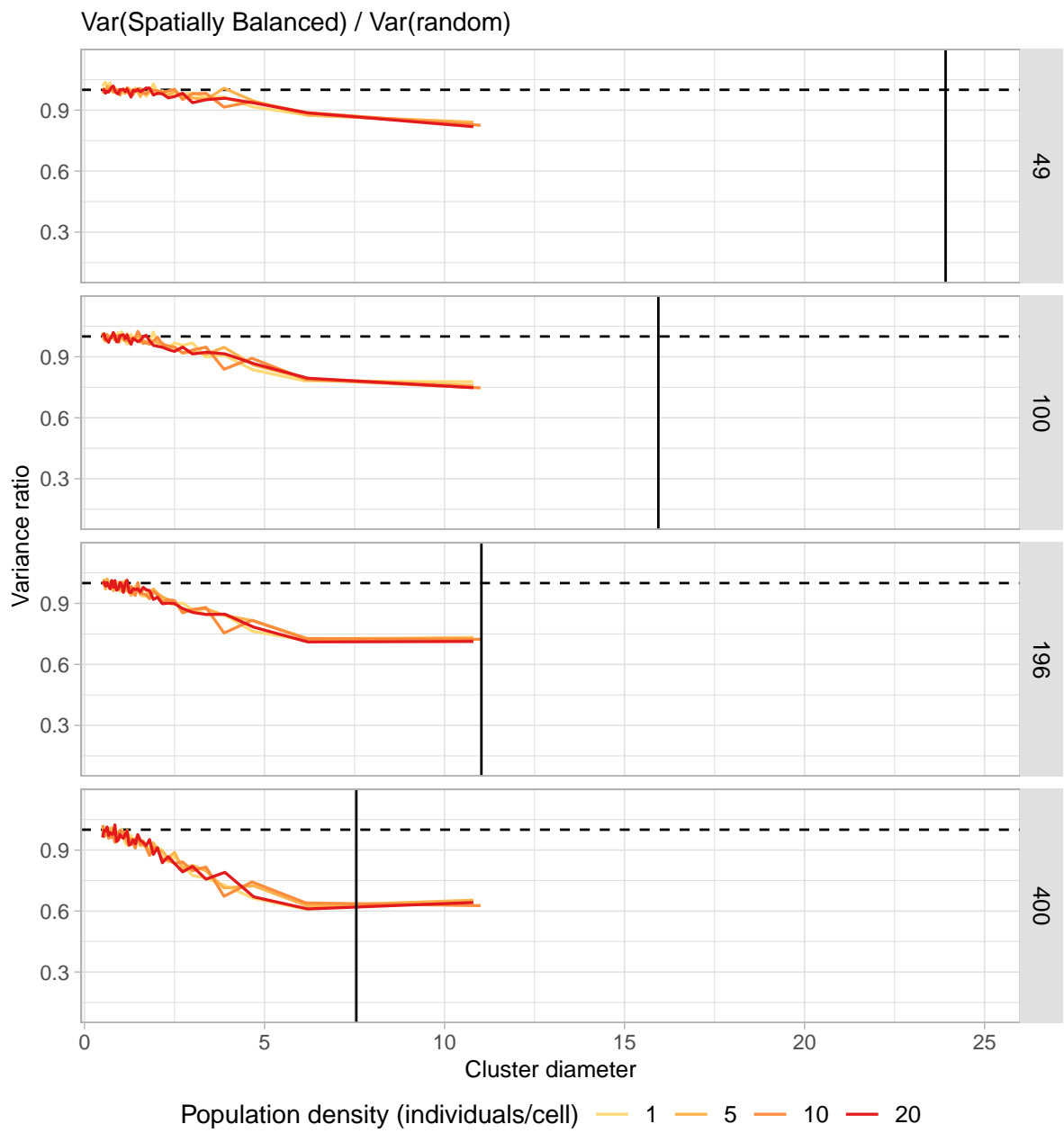
Figure S1.3: Ratio of the sampling variance of systematic sampling (SYS) over the sampling variance of simple random sampling (SRS) for the aggregated populations. The x-axis is the cluster diameter, and panels show four different sample sizes. Each curve shows the variance ratio obtained for a different mean density of individuals. The black vertical lines show the point where the distance between the sampling units is equal to the cluster diameter. Density was increased by increasing either both kappa and mu (modality 1), only kappa (modality 2) or only mu (modality 3).

SBS variance ratio as a function of cluster diameter

Modality 1



Modality 2



Modality 3

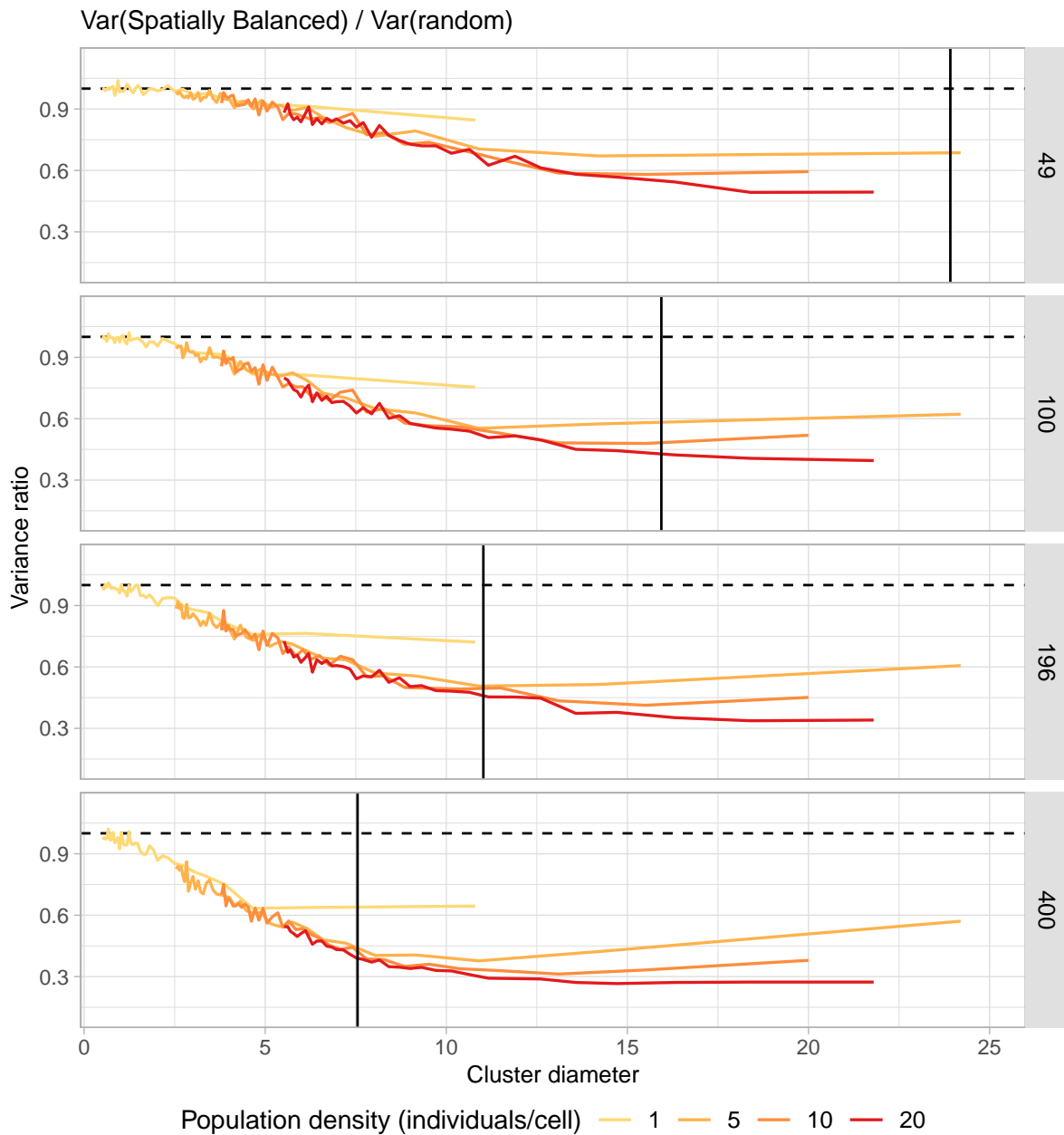


Figure S1.4: Ratio of the sampling variance of spatially balanced sampling (SBS) over the sampling variance of simple random sampling (SRS) for the aggregated populations. The x-axis is the cluster diameter, and panels show four different sample sizes. Each curve shows the variance ratio obtained for a different mean density of individuals. The black vertical lines show the point where the mean distance to the twelve nearest sampling units is equal to the cluster diameter. Density was increased by increasing either both kappa and mu (modality 1), only kappa (modality 2) or only mu (modality 3).

Appendix S2. Examples of simulated virtual populations

The examples of the simulated virtual populations are in the file “Appendix_S2_pattern_illustration.zip”. For the populations simulated using the SSI process, examples are presented for mean densities of 1, 10 and 20 individuals/cell, and levels of dispersion index $I = 0.4, 0.6$ and 0.8 . For the populations simulated using the Matérn cluster process, examples are presented for mean densities of 1, 5, 10, 15, 20, 25 and 30 individuals/cell, and levels of dispersion index of $I = 6, 15, 30, 45$ and 75 . Examples of population are presented for the three density increase modalities. For populations simulated with the Poisson process ($I = 1$), examples are presented on the same page as the populations simulated with the Matérn cluster process. For the three point processes, the same parameter values were used as for the simulations presented in the main text, but the simulation window was reduced to 25×25 (instead of 100×100) for illustrative purposes. A histogram showing the number of individuals per 1×1 cell is associated to each virtual population.

Appendix S3. Verification of lack of bias in the density estimates

For all populations, both virtual and natural, whatever the sample size, the mean density estimates resulting from the three sampling methods were always very close to the true population density. The difference between the estimated density and the true density was usually less than 0.1 individual/cell, and sometimes less than 0.01 individual/cell. This indicates that all sampling methods provided unbiased estimates, regardless of the density of the studied population, its aggregation level and the sample size used. This result was expected from sampling theory, as for the three sampling methods the sample mean is a design-unbiased estimator of the population mean, meaning that the estimates will be unbiased whatever the characteristics of the studied population (Thompson, 2012). Figure S3.1 shows the difference between the true population density and the estimated population density for the virtual populations and sampling designs presented in Figure 2 of the main text. Similar results were found for all densities we simulated, and for the three modalities used to increase population density with the Matérn cluster process.

Sample size — 9 — 15 — 25 — 49 — 100 — 150 — 196 — 300 — 400

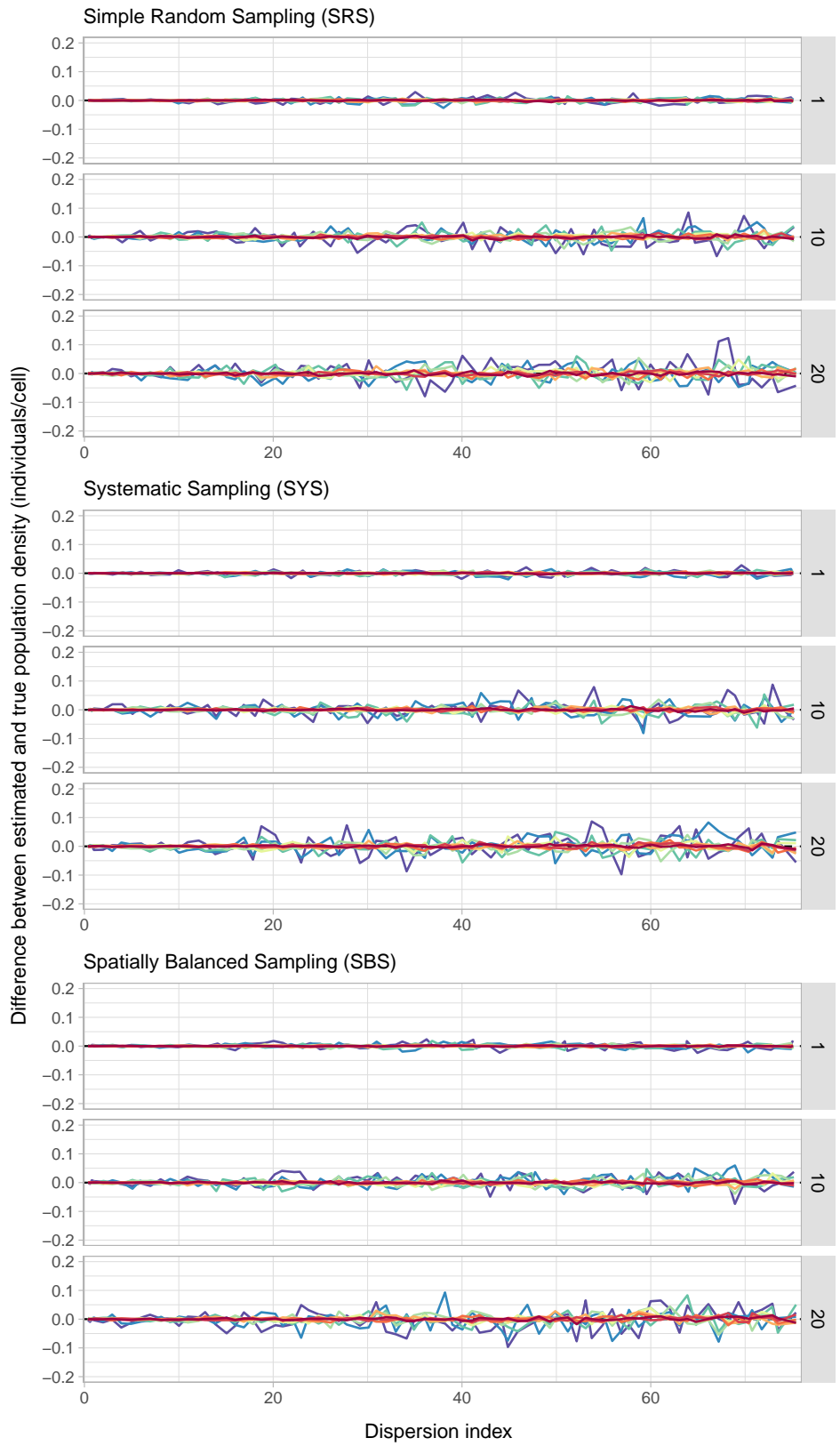


Figure S3.1: Difference between the true population density and the estimated population density obtained with simple random sampling (SRS), systematic sampling (SYS) and spatially balanced sampling (SBS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell). For the aggregated populations, density was increased by simultaneously increasing the number of clusters and the number of individuals per cluster (modality 1). Each point of the curves was obtained by computing the average over 60 populations of the difference between the true density and the mean of 1,000 sample means.

Appendix S4. Test of variance estimators

In the main text of the paper we have shown that on average SYS and SBS provide more precise or at least as precise population size estimates as SRS for aggregated populations. However, a main difficulty when using SYS (and to a lesser extent for SBS) is to obtain an accurate variance estimate from a single sample, to have a reliable estimate of the uncertainty associated to the population size estimate. We therefore assessed the performance of multiple variance estimators that have shown promising results in recent studies, and proposed an additional estimator (V_{ZIP}) that is more adapted for populations following the Matern cluster process we used to simulate our virtual populations. Our goal was to check if the gain in precision of the population size estimates we have shown is not lost because of poor variance estimators available for SYS and SBS. We performed these tests on both the virtual and the three natural populations we studied.

Take home message: As expected, for the virtual populations, the variance estimators we selected from previous studies for SYS overestimated sampling variance when the distance between the sampling units was close to the mean cluster diameter. Conversely, our estimator V_{ZIP} was almost unbiased under these conditions, but it underestimated variance for higher aggregation levels. For SBS, the most commonly used estimator in the literature (V_{nbh}) had relatively good performances. For the natural populations using SYS or SBS, both some estimators from previous studies and our V_{ZIP} estimator performed well, yielding almost unbiased estimates of sampling variance. Overall, using SYS or SBS instead of SRS with a variance estimator that is appropriate for the studied population will generally result in a substantial gain in ‘apparent’ precision, although this gain will usually be slightly smaller than the gain in true precision.

Methods

The variance estimators we selected for this study are presented in Table S4.1. For SBS, a single estimator (V_{nbh}) was identified as the best performing in all studies (e.g. Grafstrom et al., 2012; Robertson et al., 2013). For SYS, we chose the best performing estimators among the 16 that have been tested in three recent studies (McGarvey et al., 2016; Magnussen & Fehrmann, 2019; Magnussen et al., 2020).

All these estimators are based on the same principle: compute the sample variance and a correlation metric of the abundance among neighbouring sample units; use the correlation metric to weight the sample variance. Several correlation metrics (e.g. Moran’s I for V_w , Geary’s C for V_{str2}) and several definitions of the neighbourhood (e.g. the 4 closest units, all units within a given radius) are possible, but apart from that, the principle remains the same. Thus, these estimators are relevant only when there is correlation of abundance among neighbouring units in the sample.

Yet for our virtual populations simulated using a Matern process, when sampling with SYS (and to a lesser extent SBS), for sample sizes for which the distance between the sampling units is equal to the diameter of the clusters (allowing the largest gain in precision compared to SRS), there is no correlation between the neighbouring units included in the sample. Indeed, under these conditions, there can only be one sample unit per cluster, and as the position of the clusters is random, whether a unit is in a cluster or not is independent of whether its neighbouring units are in a cluster or not. Therefore, the estimators using the correlation between neighbouring units in the sample will considerably overestimate the sampling variance under these conditions. In addition, the individuals inside clusters are randomly located, i.e. following a Poisson process. We have therefore proposed a new variance estimator that is better adapted to populations where individuals are grouped in well-defined clusters.

Our new estimator is based on the hypothesis that sampling a population where individuals are grouped into well-defined clusters and where there are no individuals outside these clusters using SYS or SBS is equivalent to randomly drawing a sample in a Zero-Inflated Poisson distribution (ZIP). Indeed, the sampling units in the clusters approximately follow a Poisson distribution, and the sampling units outside the clusters constitute an excess of zeros with respect to this Poisson distribution. The computation of our estimator (called V_{ZIP}) is performed in three steps:

1. Estimate the two parameters of the ZIP distribution (λ , the expected mean of the Poisson distribution, and π , the probability of extra zeros) from the sample by maximum likelihood (Beckett et al., 2014; Jackman et al., 2020).

2. Compute the population variance estimate using lambda and pi using the following formula : $S_{\text{hat}}^2 = \lambda * (1 - \pi) * (1 + \pi * \lambda)$
3. Compute the sampling variance estimate from the population variance based on the hypothesis that the sample was drawn randomly: $v_{\text{ZIP}} = (S_{\text{hat}}^2 / n) * (1 - n/N)$

Table S4.1: Summary of the variance estimators we tested.

Notation	Sampling method	Source	Performance tests	Why we choose it
V_textbook	SRS, SYS and SBS	Cochran (1977) eq. (2.20) p. 26	McGarvey et al. (2016) ; Magnussen & Fehrmann (2019) ; Magnussen et al. (2020)	Used as benchmark in all papers studying the performance of variance estimators.
V_8	SYS	Wolter (2007) eq. (8.2.9) p. 302	McGarvey et al. (2016)	One of the two best performing estimators among the 13 tested in McGarvey et al. (2016).
V_w	SYS	D'Orazio (2003) table 2 & eq. (4.3) p. 284 & 285	McGarvey et al. (2016)	One of the two best performing estimators among the 13 tested in McGarvey et al. (2016).
V_str2	SYS	D'Orazio (2003) eq. (4.1) and (4.2) p. 285	Magnussen & Fehrmann (2019) ; Magnussen et al. (2020)	One of the two best performing estimators among the five tested in Magnussen et al. (2020) that did not show a tendency to underestimate variance.
V_nbh	SBS	Stevens & Olsen (2003)	Grafstrom et al. (2012) ; Robertson et al. (2013)	The best performing estimator in Grafstrom et al. (2012) and Robertson et al. (2013).
V_ZIP	SYS and SBS			The variance estimator we propose, better adapted to populations following a Matern cluster process than the other estimators which are based on the correlation between neighbouring sampling units.

To evaluate the performance of these estimators, we ran the same simulations as for the main text of the article for both the virtual and natural populations, and for each simulated sampling survey, we computed the variance estimated from the sample with each estimator, and computed the associated 95% confidence interval.

To save computation time, for the virtual populations we kept only one level of dispersion index out of two, we ran the simulations for 20 populations instead of 60 for each combination of density and aggregation, and realised 600 sampling surveys per population instead of 1,000. For SYS, some of the estimators we selected are not applicable when the units cannot be arranged in a square grid, so we removed the sample sizes of $n = 15, 150$ and 300 .

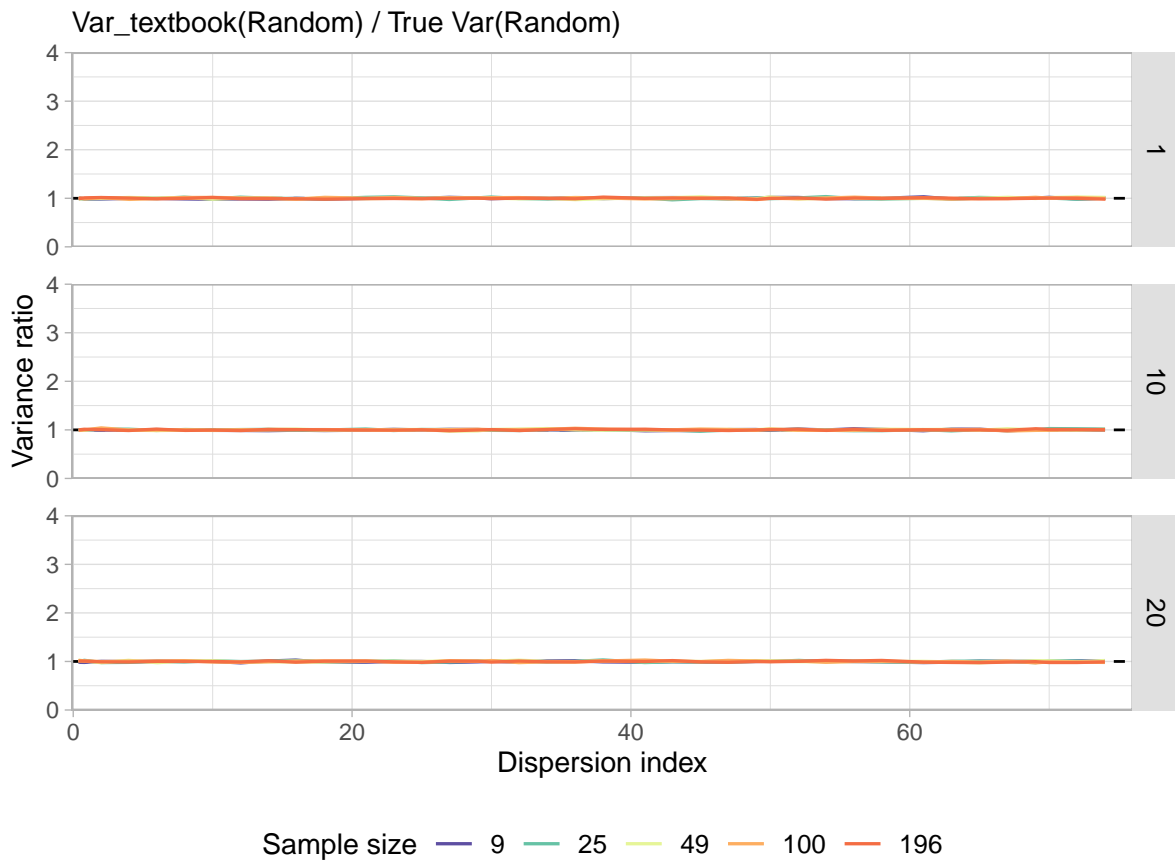
For both virtual and natural populations, we present below the following results: 1. The ratio of the estimated variance (averaged over all the sampling surveys) using each estimator over the true sampling variance to check whether the variance estimates are **biased or not**. 2. The **coverage ratio** obtained with each estimator, which is the proportion of sampling survey simulations for which the true mean density of individuals was within the 95% confidence interval (CI) of the density of individuals estimated using a given

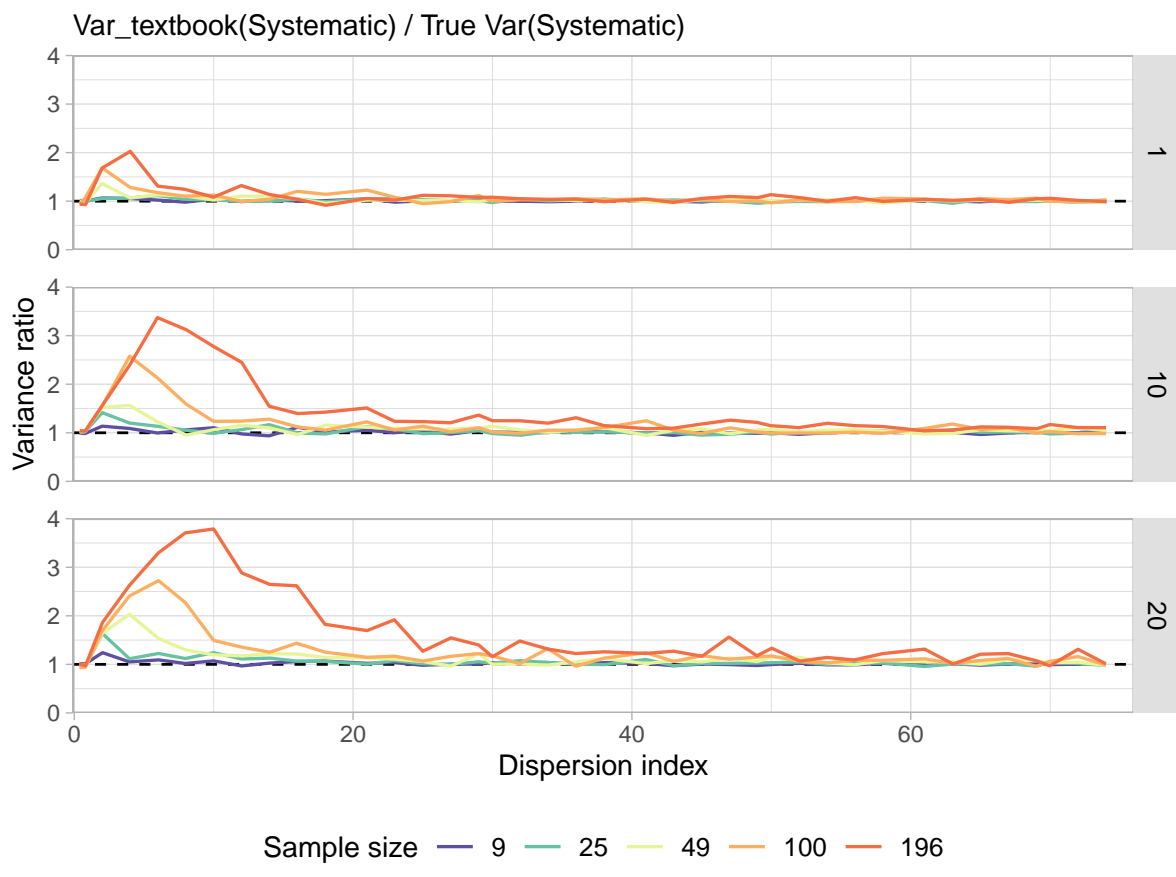
variance estimator. 3. The ratio of the variance estimated using each variance estimator for SYS and SBS over the variance estimated using the “textbook” estimator for SRS, to show in which situations using SYS or SBS instead of SRS will allow for an “**apparent**” gain in precision.

1. Virtual populations

1.1 Comparison of estimated variance and true variance

In this section, we compare the mean variance estimates obtained with the variance estimators to the true sampling variances. Only the mean variance estimate is used and there is no measure of estimate precision. Thus, the figures below only allow to assess the average lack of bias of the variance estimators and not their precision. For the assessment of the variance estimate precision, see the next section about the estimator coverage ratio.





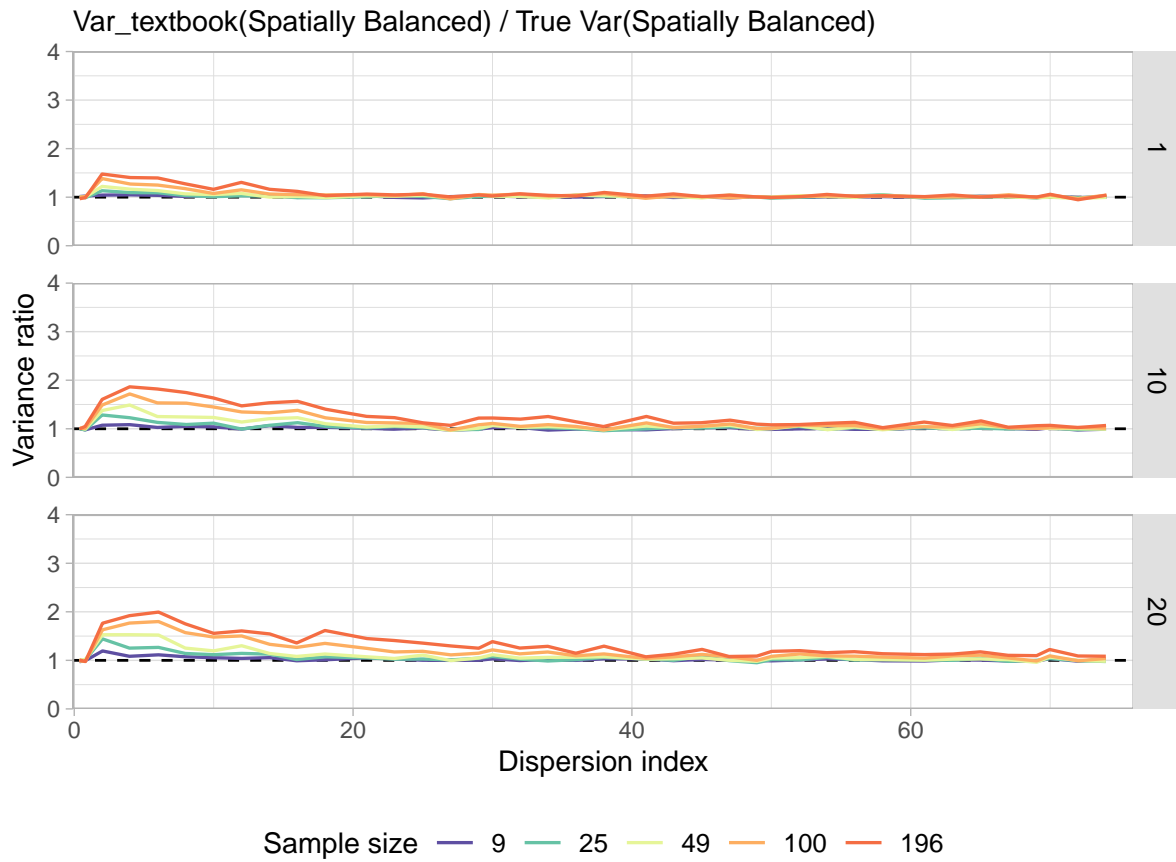
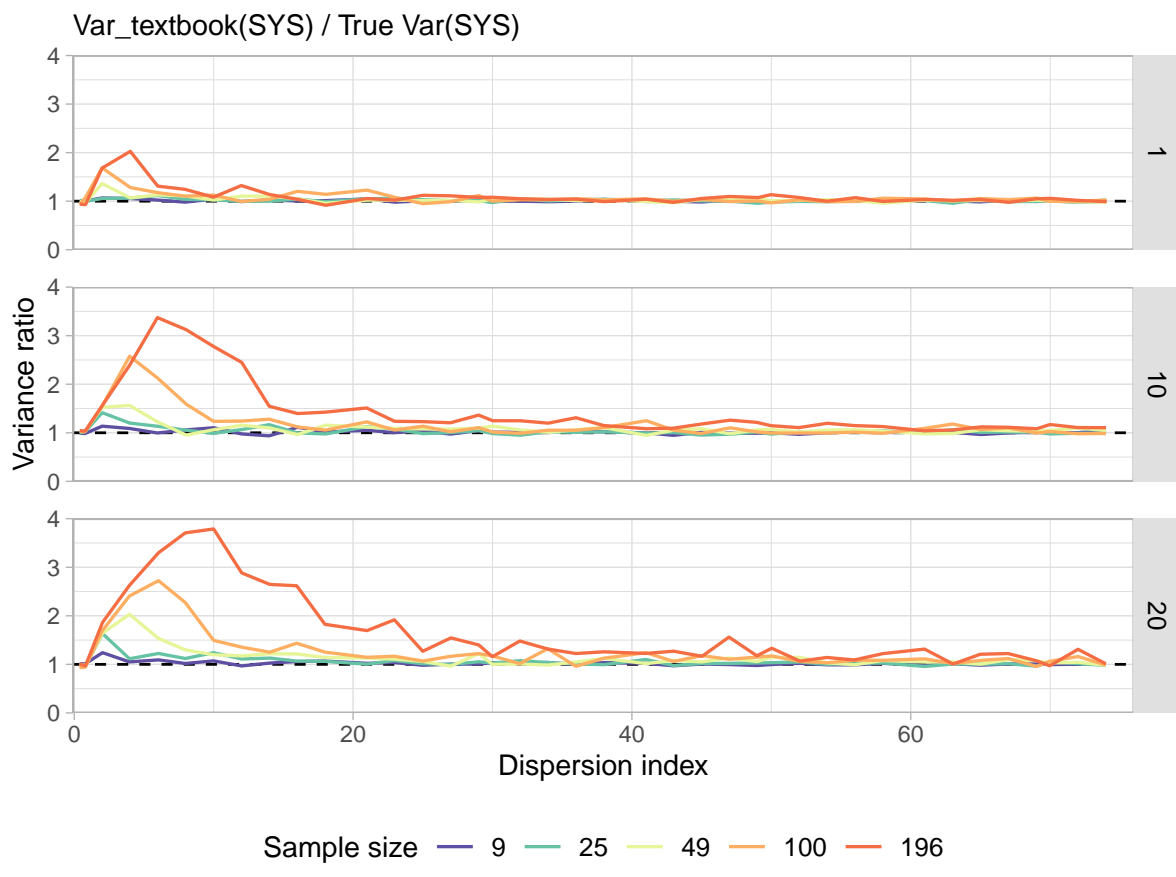
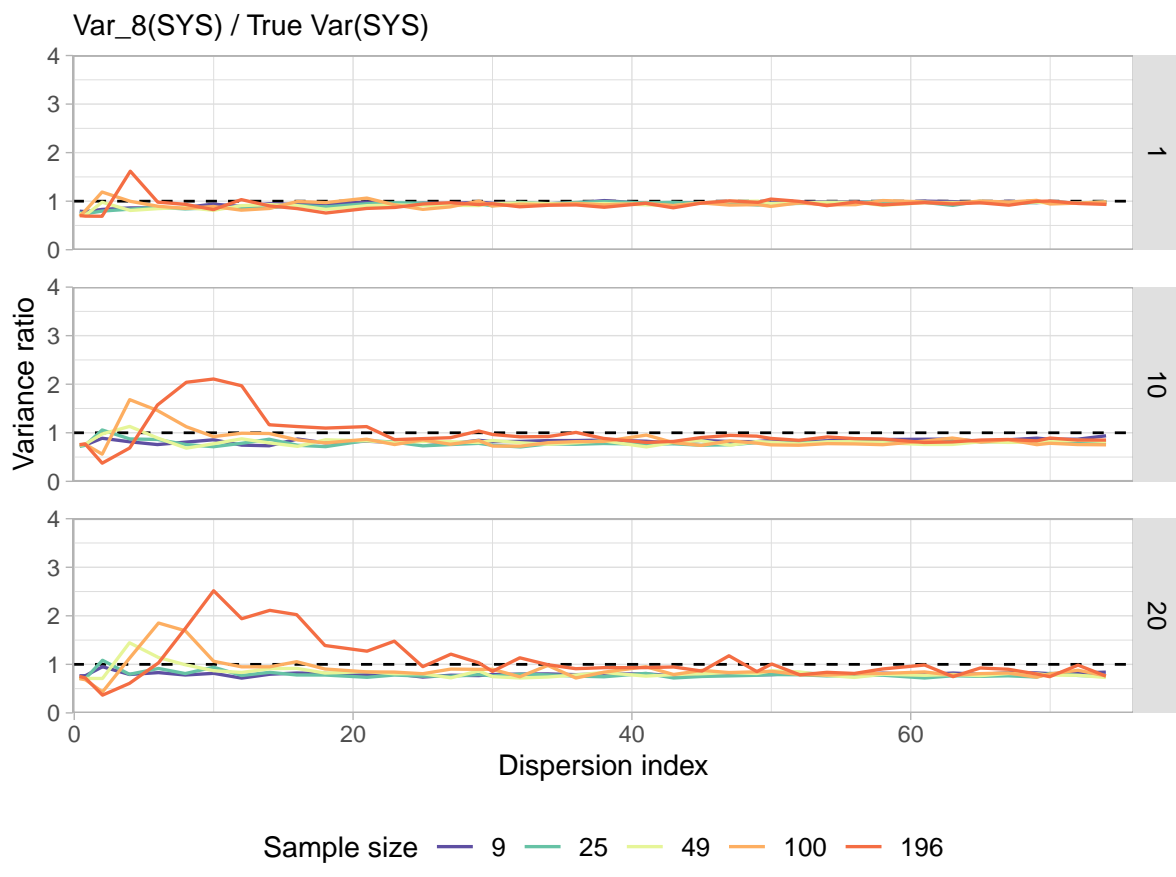
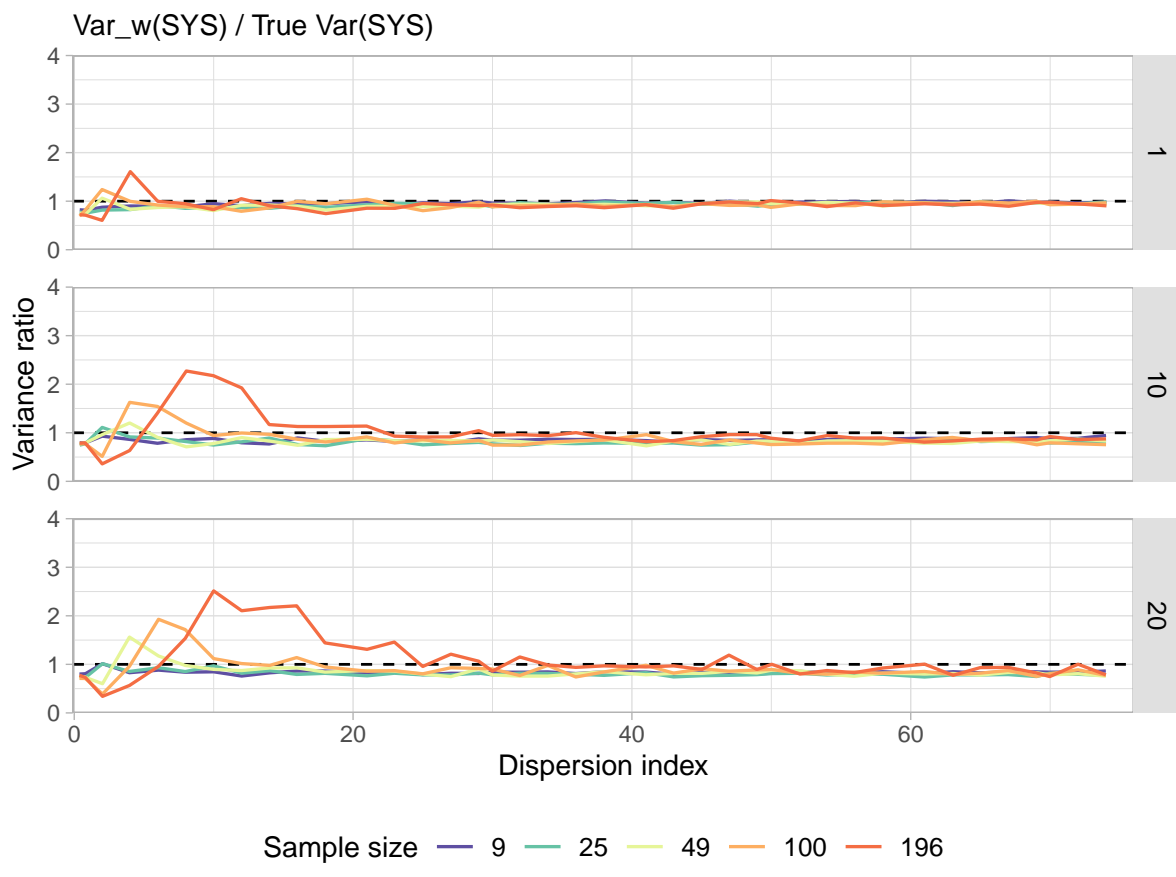
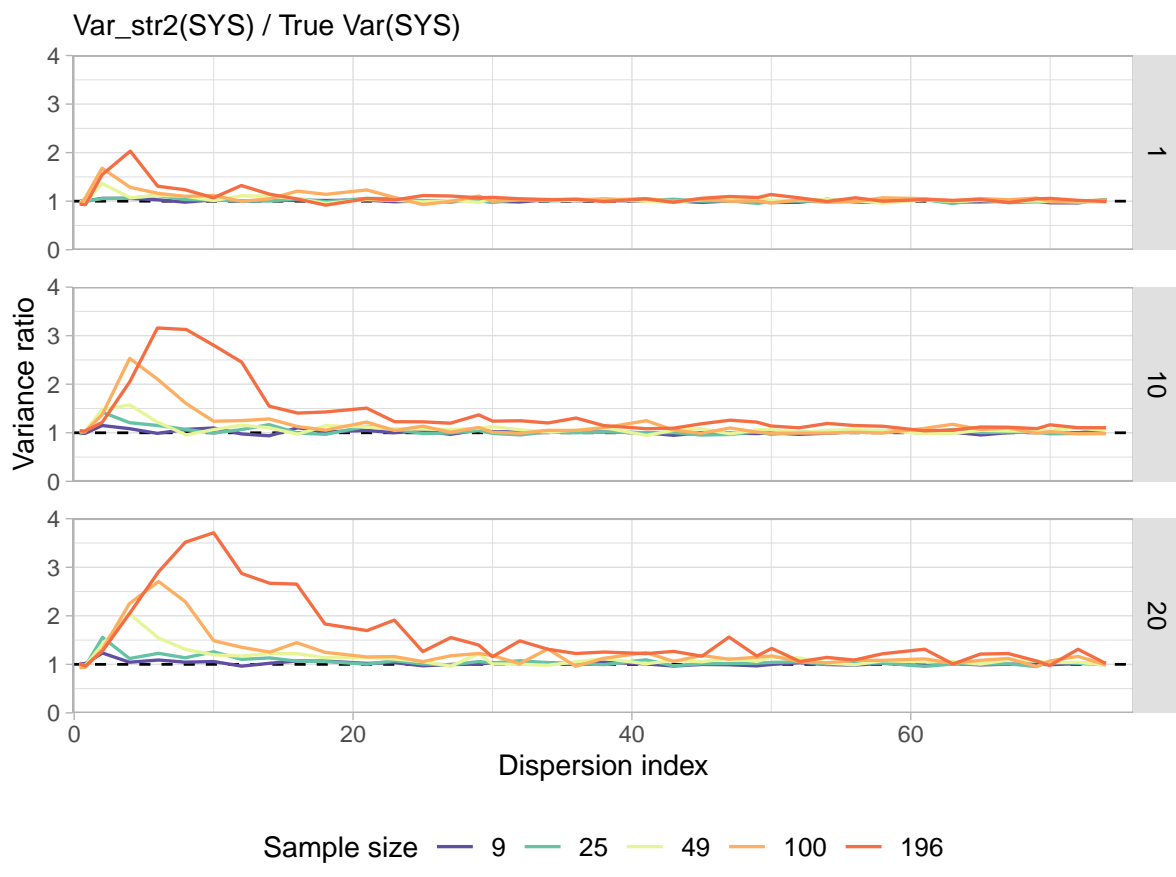


Figure S4.1: Ratio of the estimated sampling variance using the “textbook” estimator over the true sampling variance for simple random sampling (SRS), systematic sampling (SYS) and spatially balanced sampling (SBS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell). For the populations simulated using the Matern process, density was increased by increasing both kappa and mu (modality 1). Each point of the curves was estimated from 1,000 samples drawn for 20 populations. As expected from sampling theory, using the “textbook” estimator for SYS and SBS leads to a strong overestimation of the sampling variance.









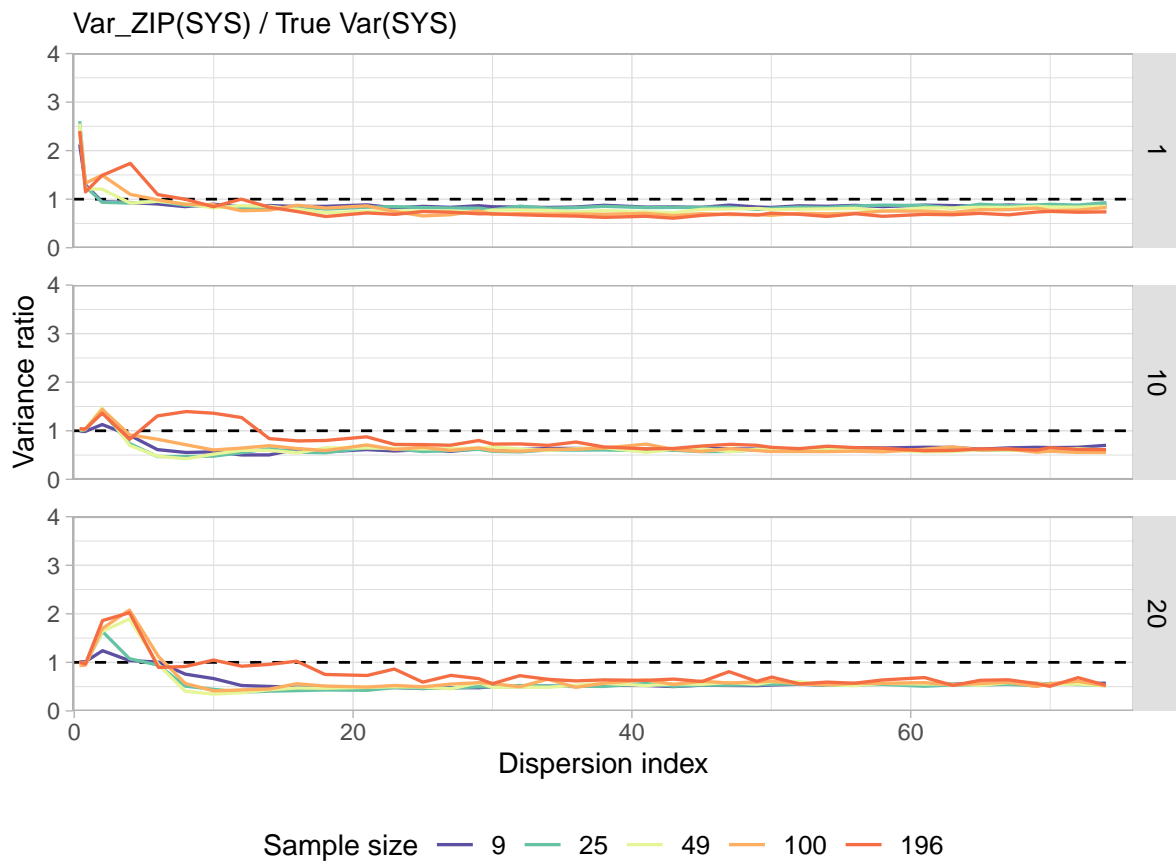
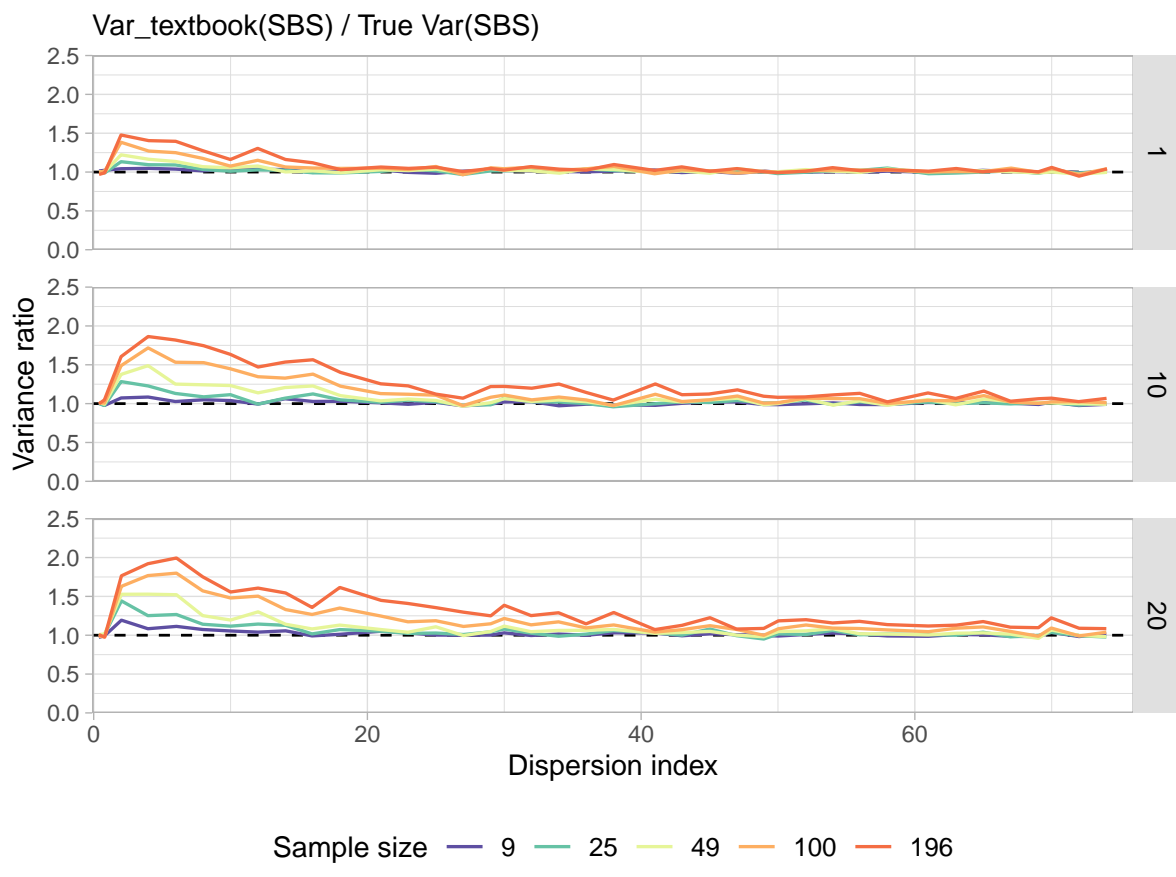
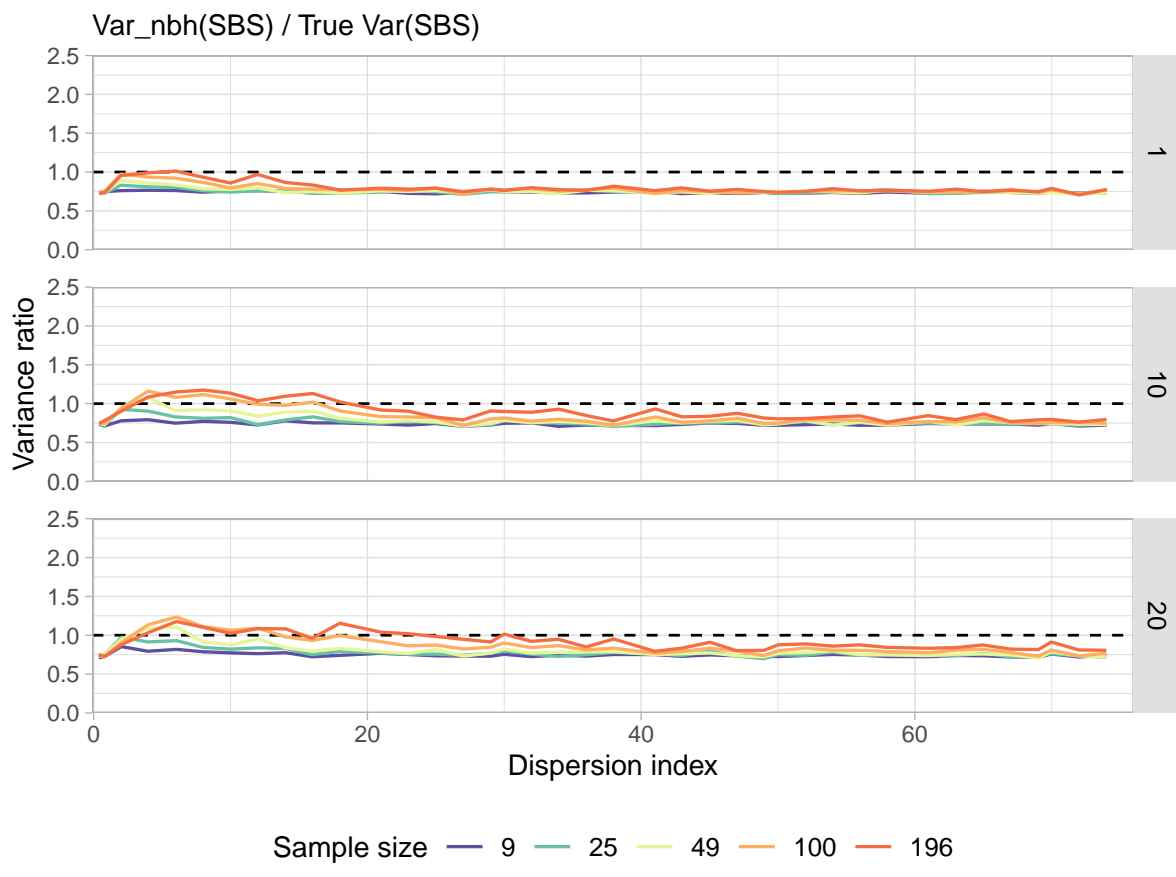


Figure S4.2: Ratio of the estimated sampling variance using five variance estimators (V_{textbook} , V_8 , V_w , V_{str2} , V_{ZIP}) over the true sampling variance for systematic sampling (SYS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).





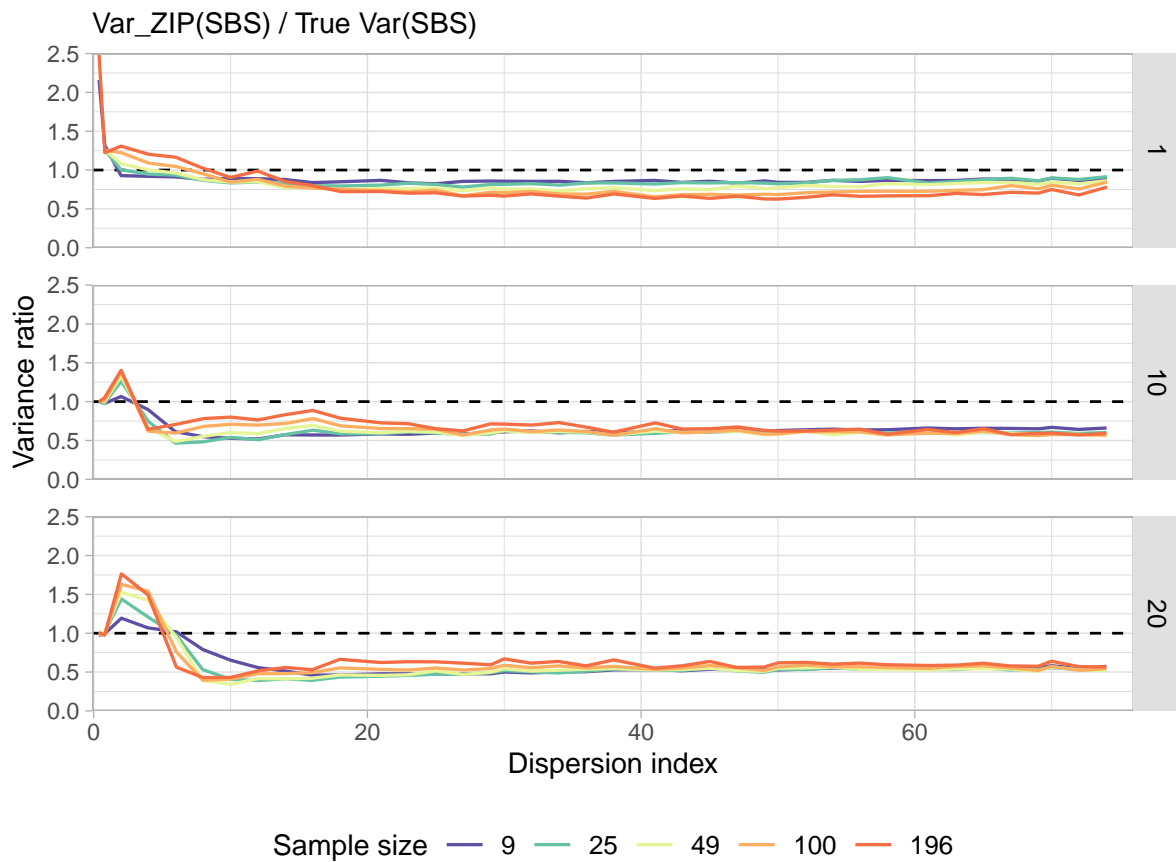


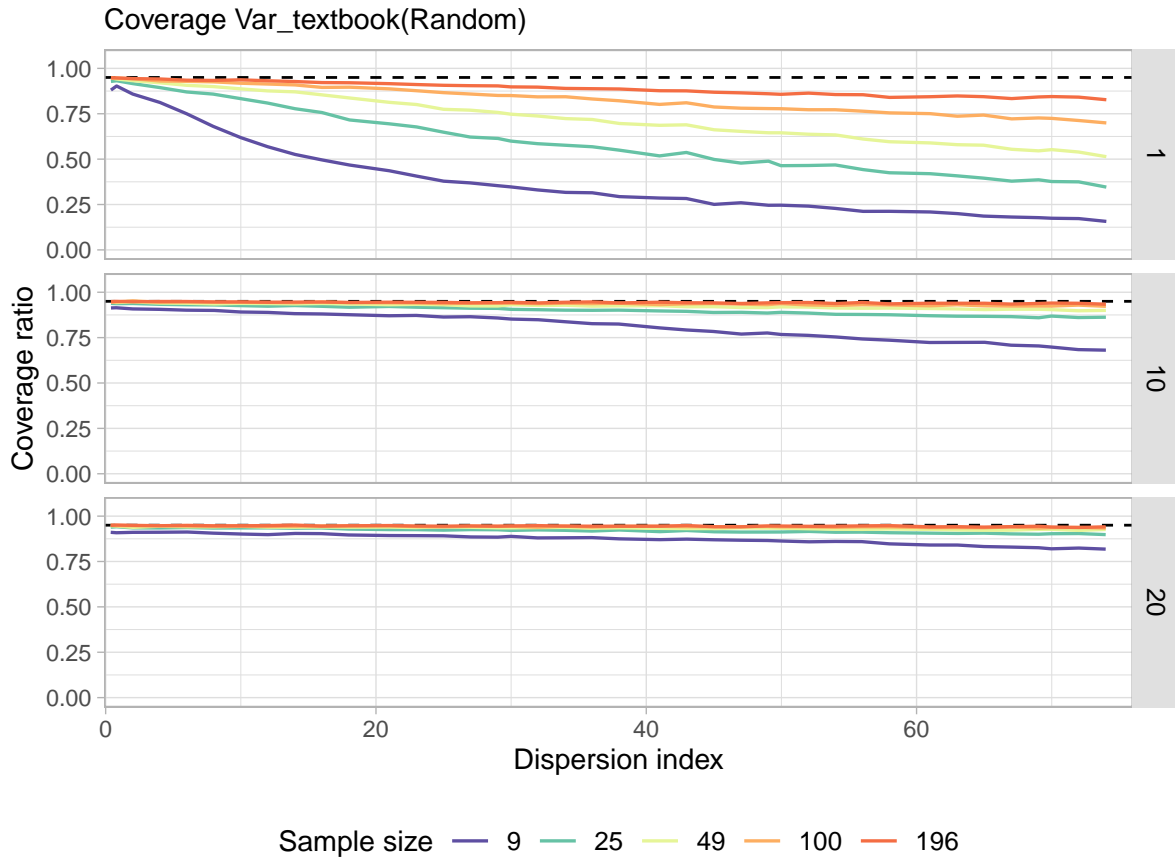
Figure S4.3: Ratio of the estimated sampling variance using three variance estimators (V_{textbook} , V_{nbh} and V_{ZIP}) over the true sampling variance for spatially balanced sampling (SYS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).

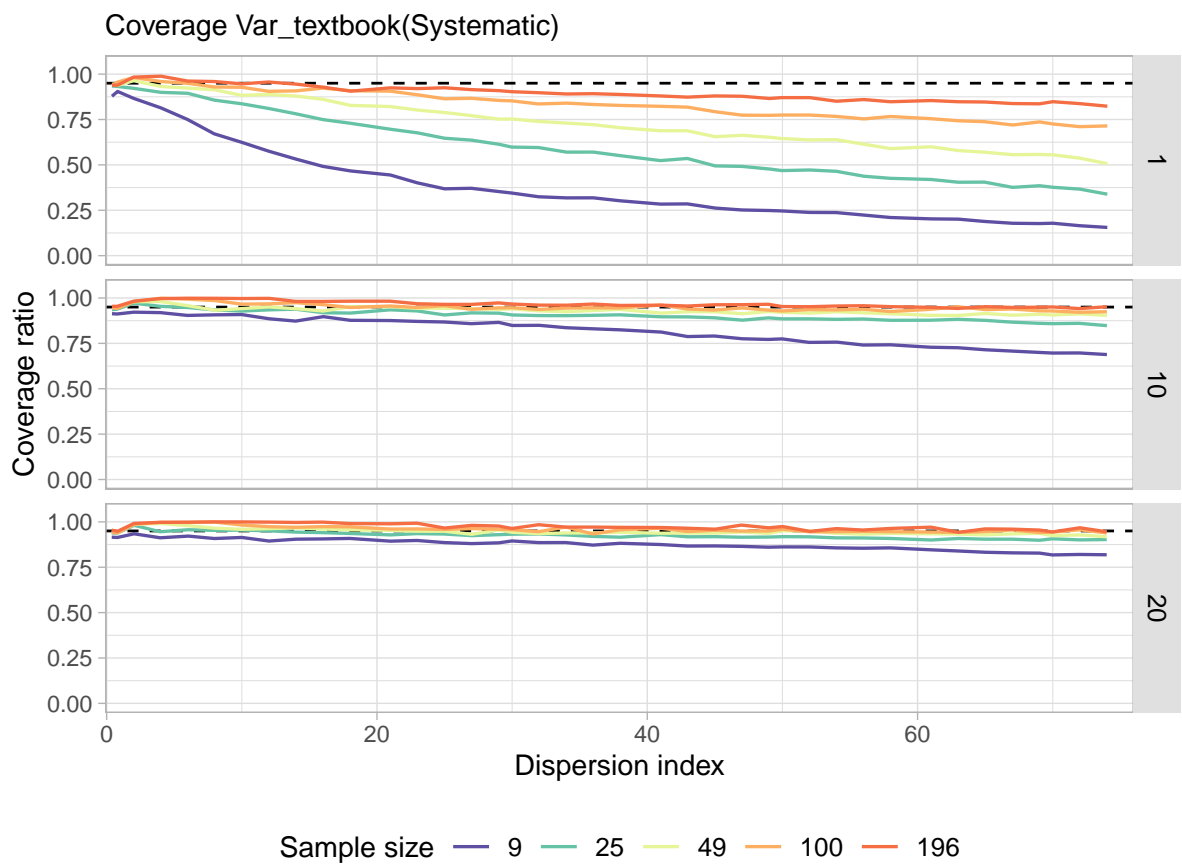
Interpretation:

- As expected from sampling theory, the textbook estimator is unbiased for SRS and tends to overestimate sampling variance for SYS and SBS (Cochran, 1977).
- For SYS, the three alternative estimators based on correlation of abundance between neighbouring units substantially overestimate the sampling variance at the levels of aggregation where SYS yields the highest increase in precision relative to SRS, i.e. where the distance between sampling units is close to the cluster diameter. Besides these levels of aggregation where all estimators overestimate the variance, V_{8} and V_{w} underestimate the sampling variance by about 10-20%, while V_{textbook} and V_{str2} are unbiased.
- For SBS, the V_{nbh} estimator underestimates the sampling variance by about 20% excepted for the higher sample sizes and for the levels of aggregation where SYS yields the highest increase in precision relative to SRS.
- For SYS, the **V_{ZIP} estimator is the only one to be nearly unbiased** at the aggregation levels where SYS yields the highest increase in precision relative to SRS. Yet for higher aggregation levels, it underestimates the variance by about 40-50%. For SBS, the V_{ZIP} estimator is overall more biased than V_{nbh} .

1.2 Estimator coverage ratio

In this section, we present the coverage ratio yielded by each variance estimator. The coverage ratio is defined as the proportion of sampling survey simulations for which the true mean density of individuals was within the 95% confidence interval (CI) of the density of individuals estimated using a given variance estimator.





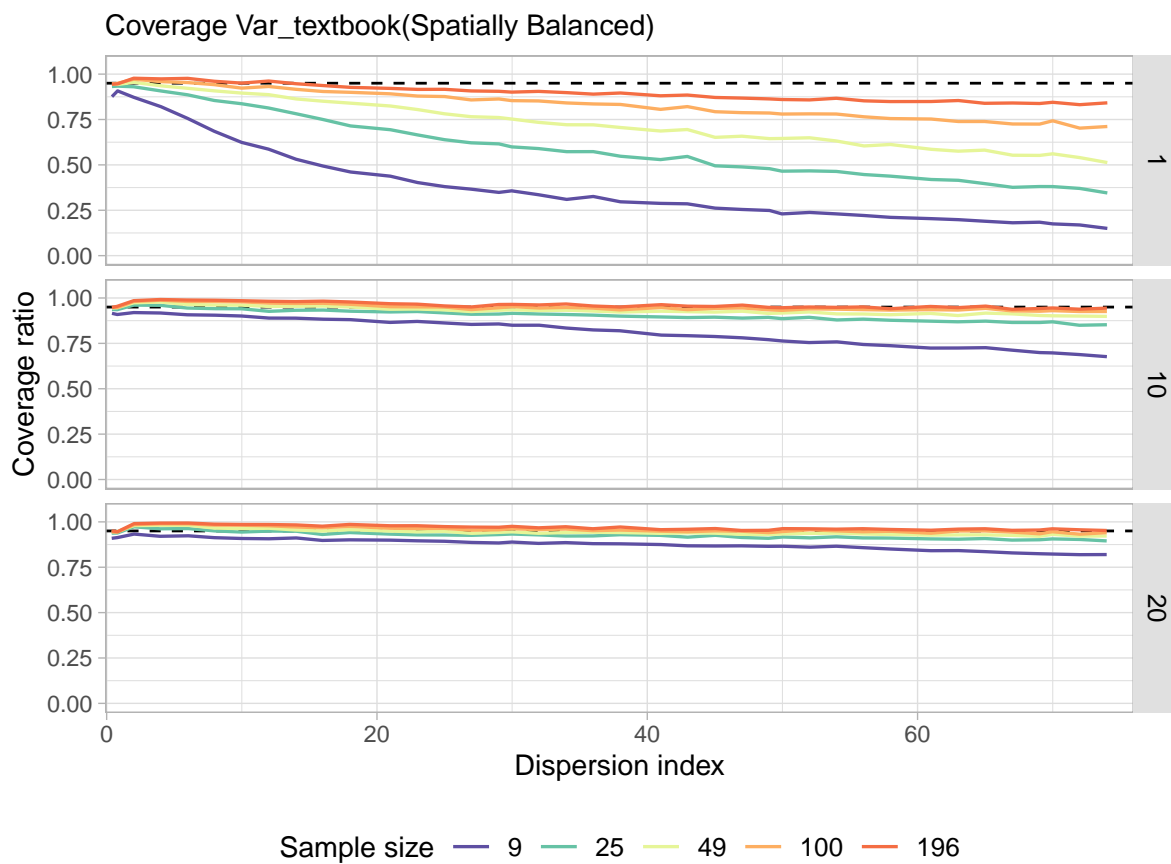
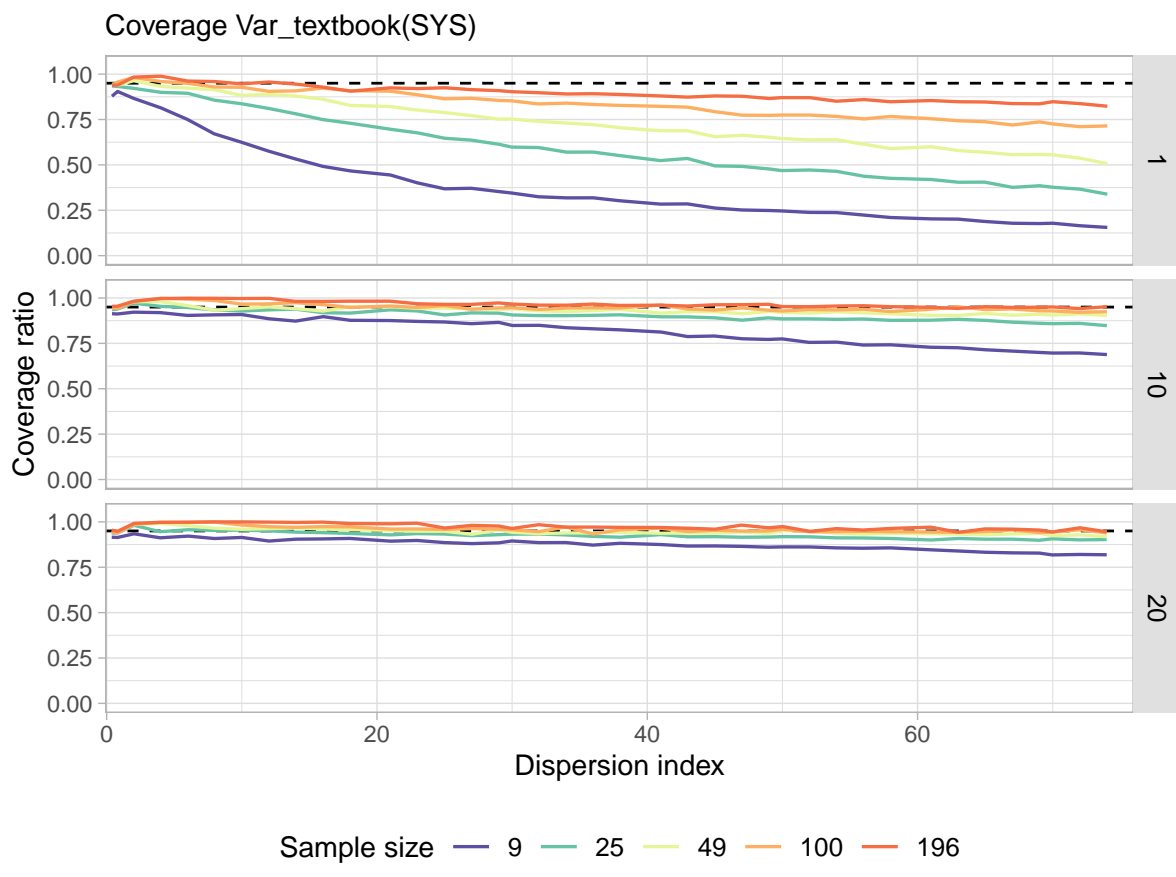
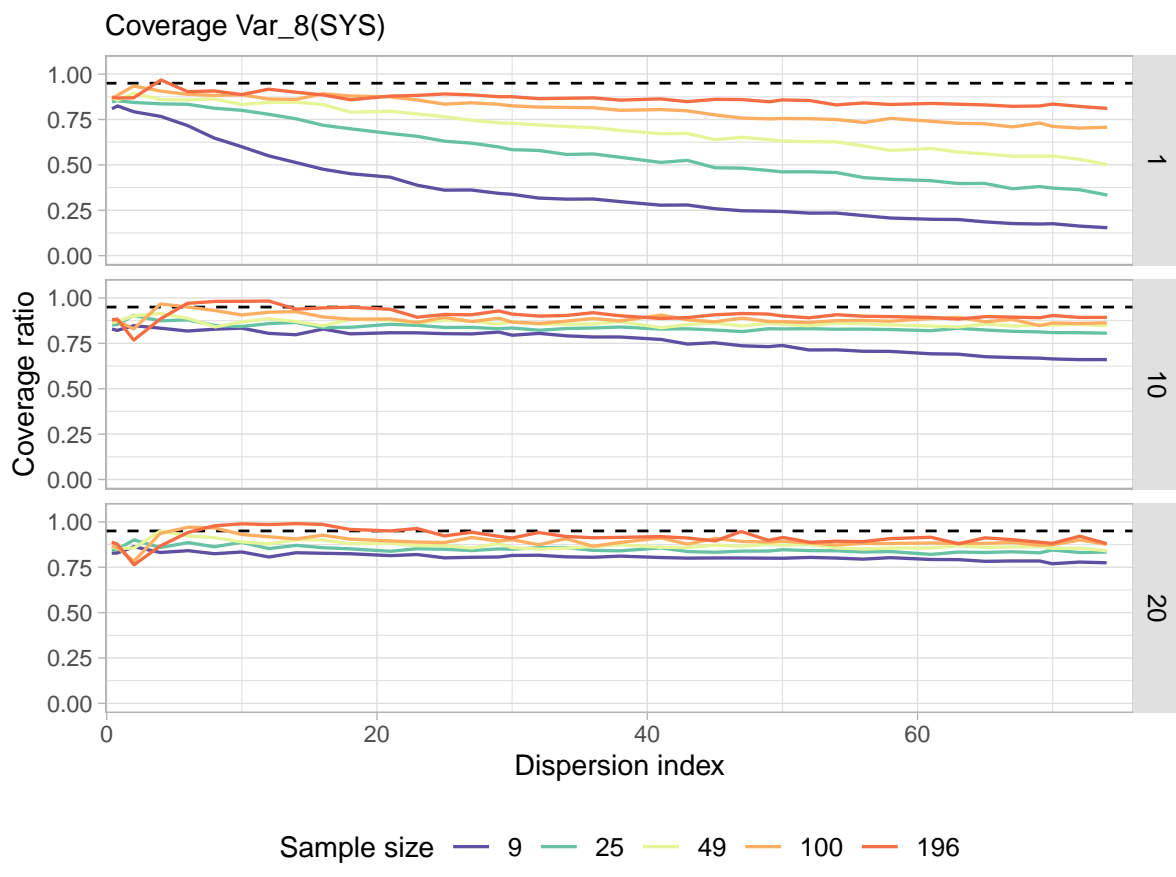
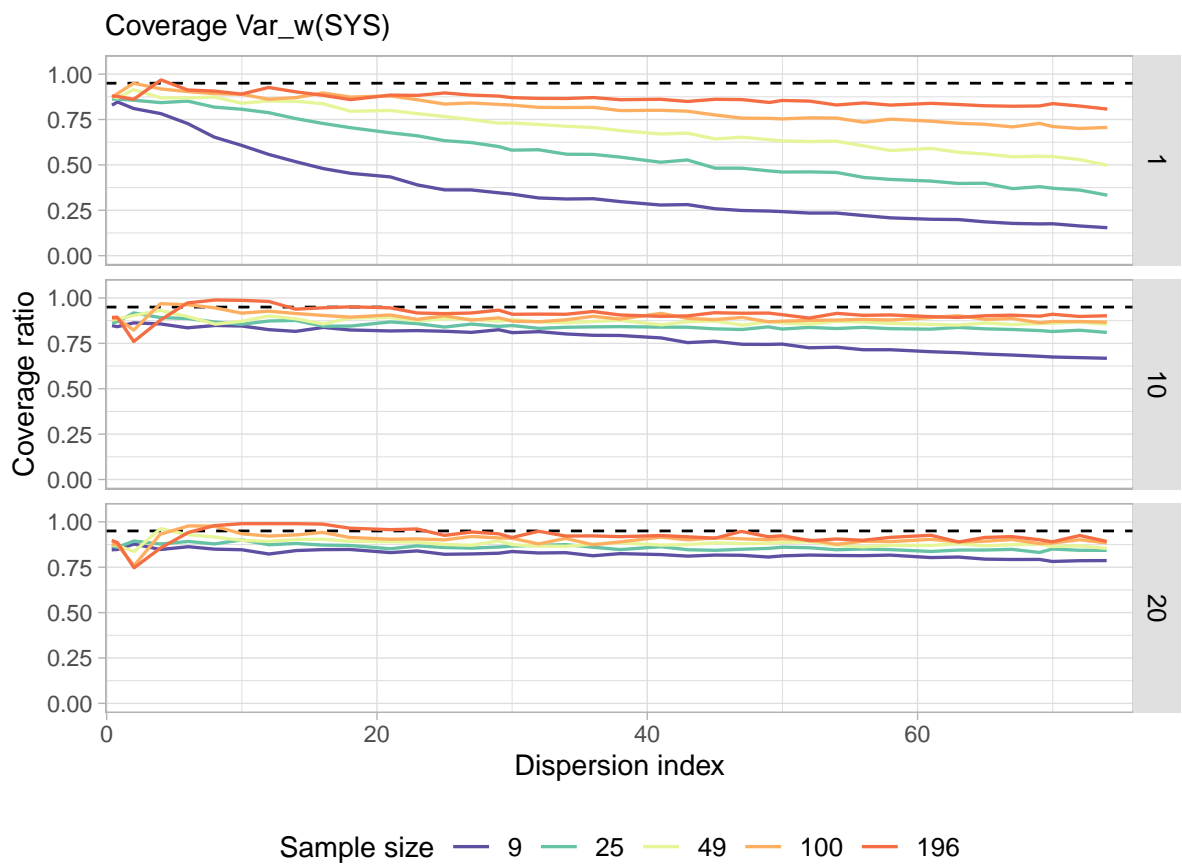
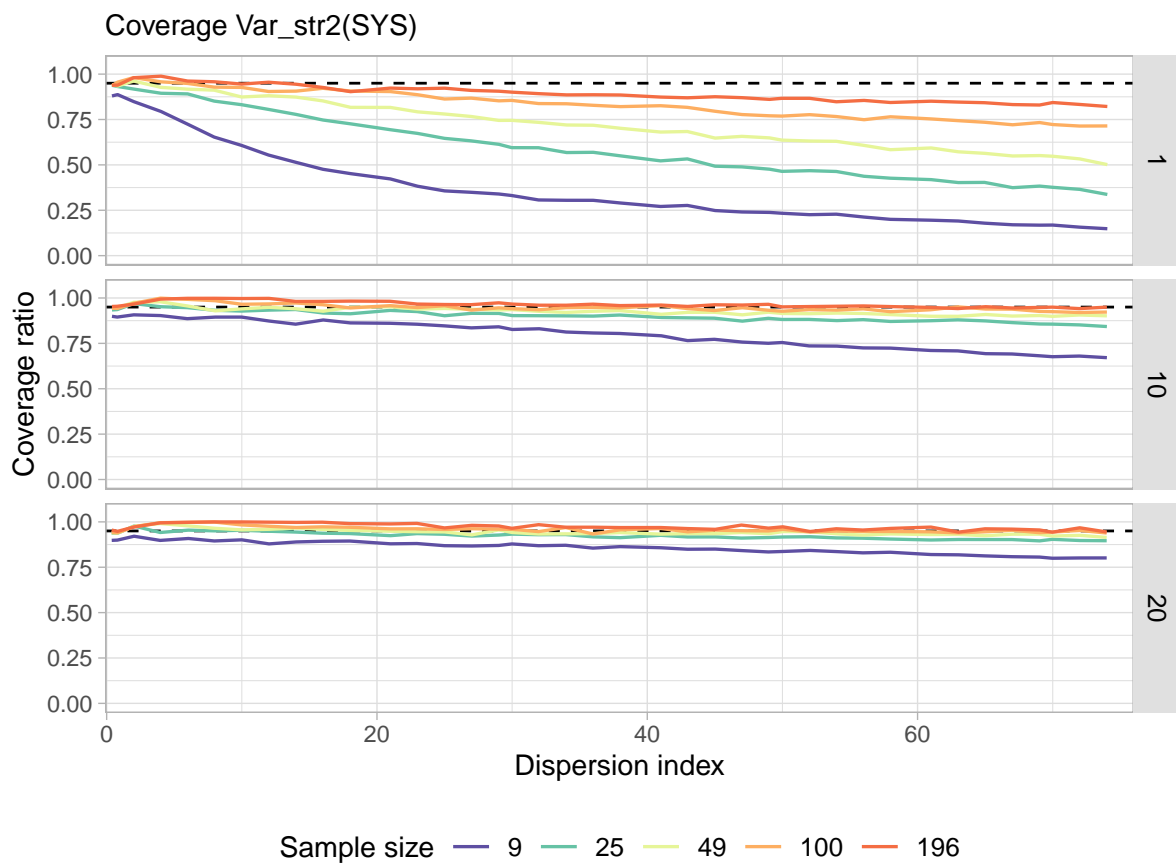


Figure S4.4: Coverage ratio of the “textbook” estimator for simple random sampling (SRS), systematic sampling (SYS) and spatially balanced sampling (SBS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).









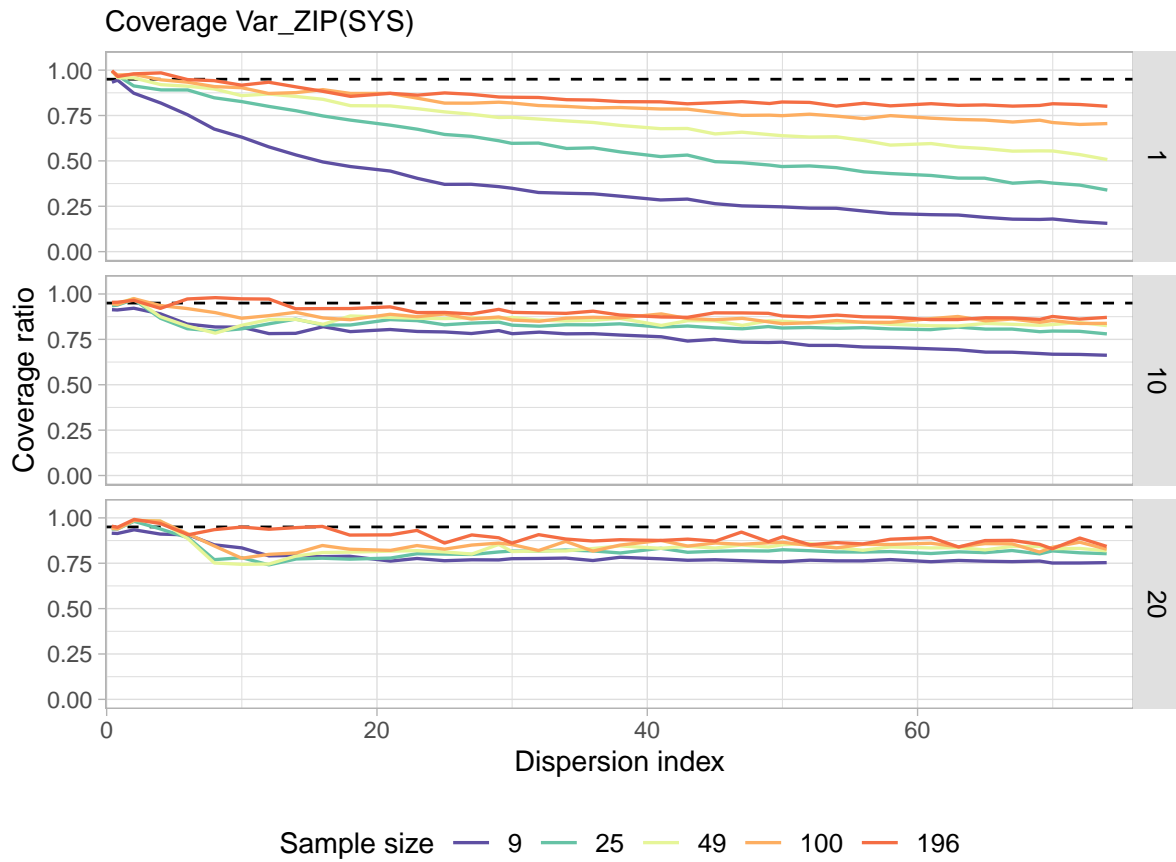
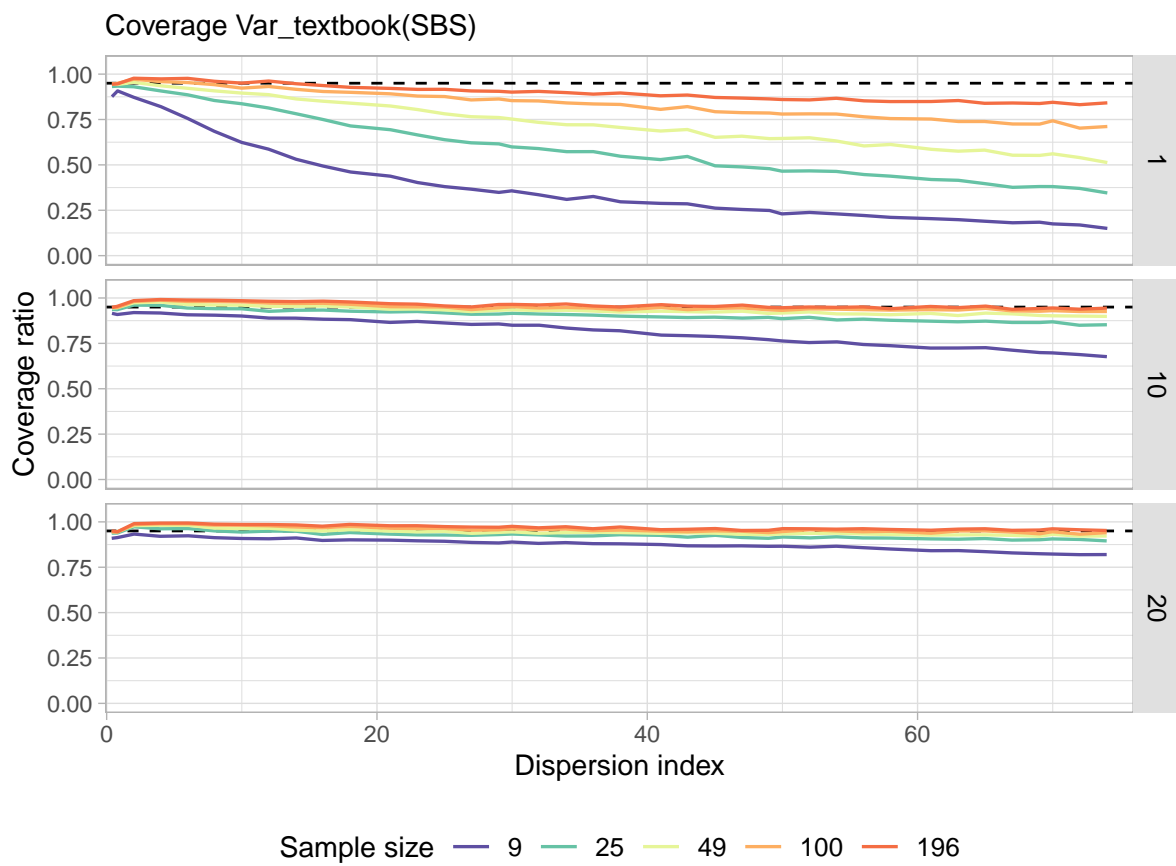
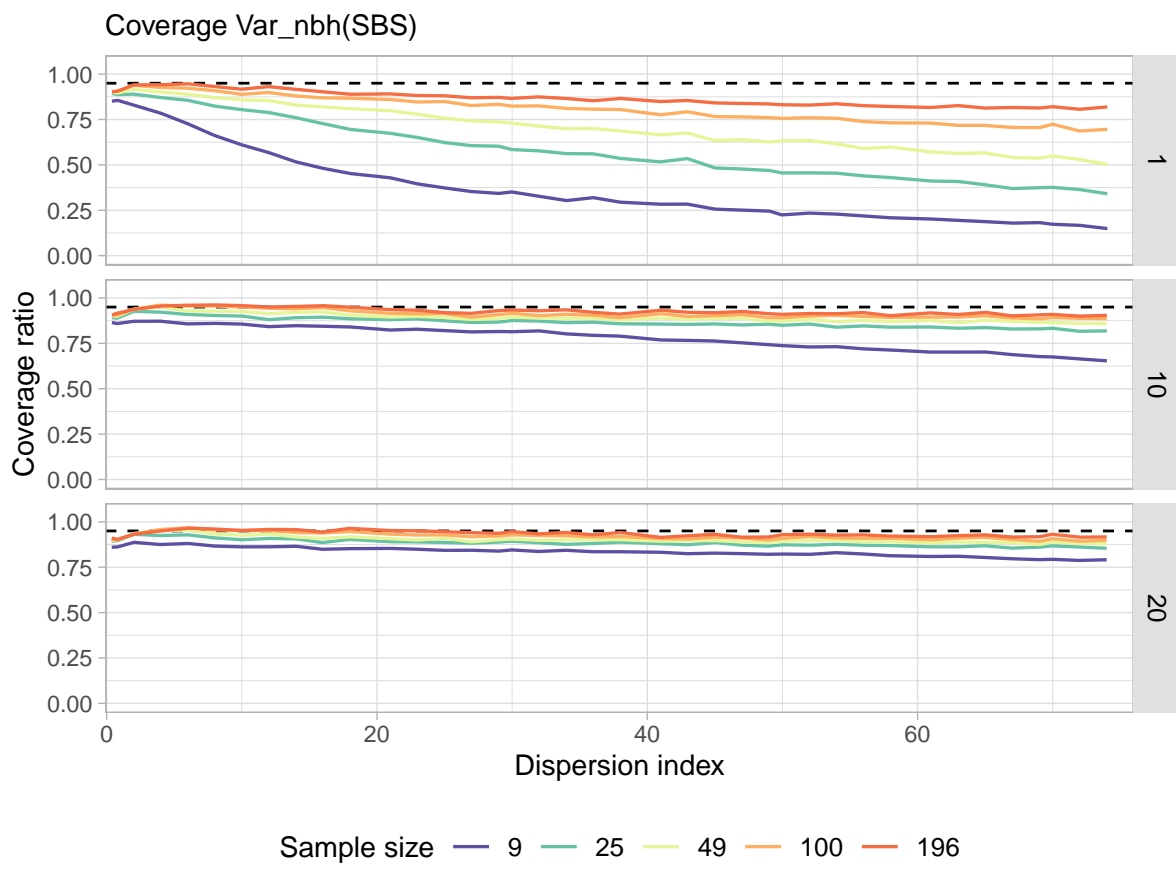


Figure S4.5: Coverage ratio of five variance estimators (V_{textbook} , V_8 , V_w , V_{str2} , V_{ZIP}) for systematic sampling (SYS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).





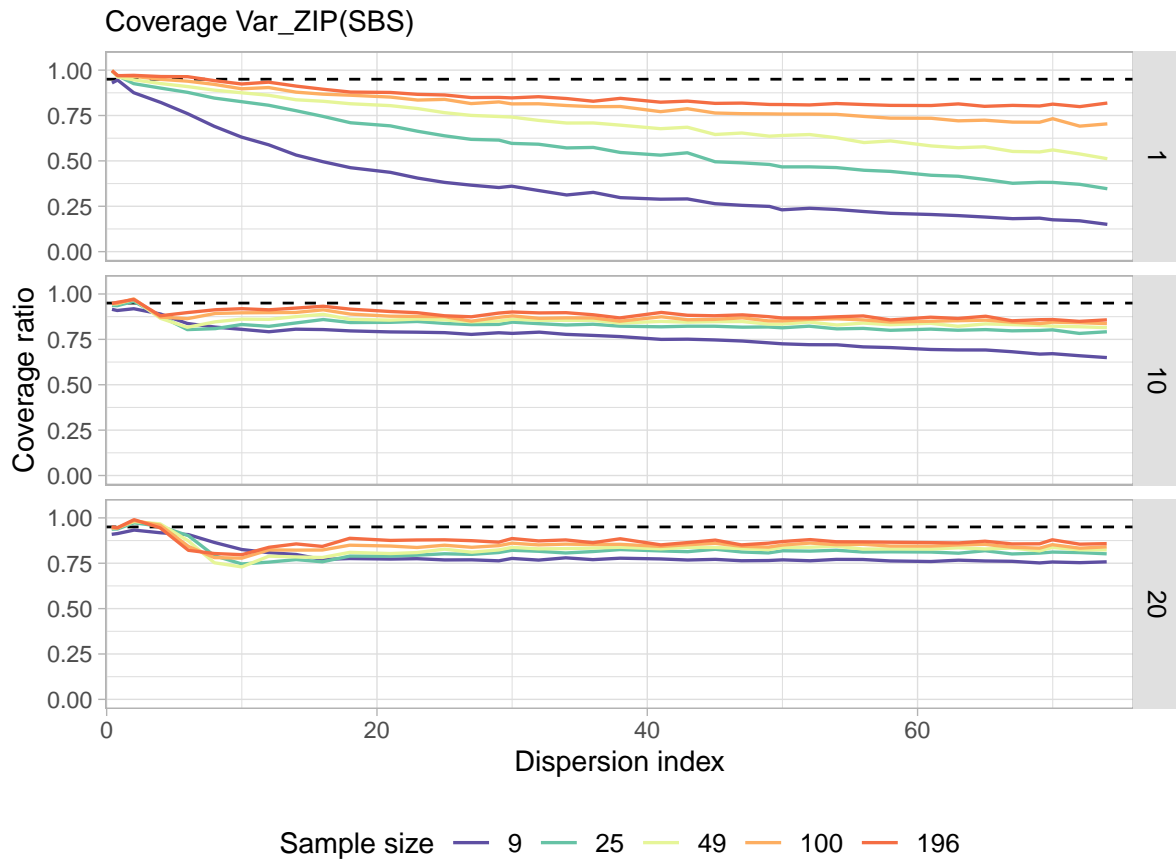


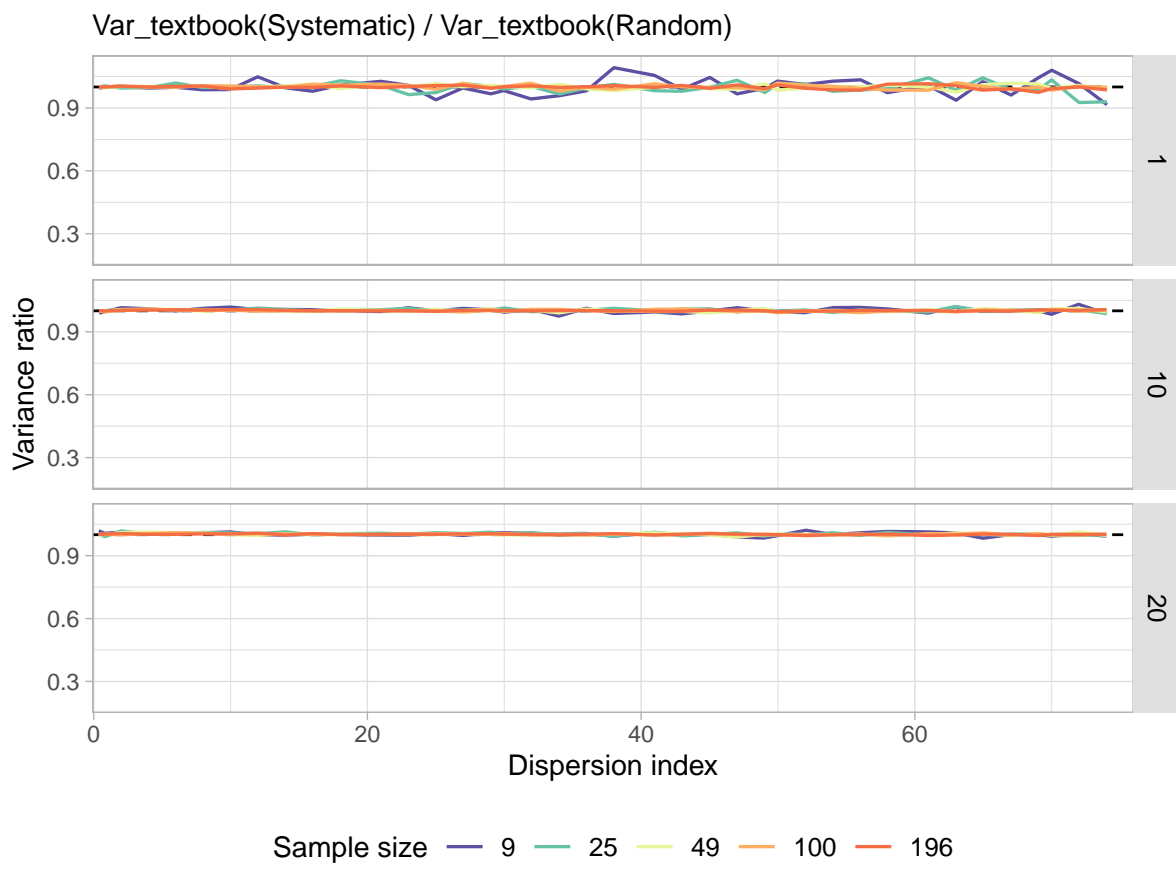
Figure S4.6: Coverage ratio of three variance estimators (V_{textbook} , V_{nbh} and V_{ZIP}) for spatially balanced sampling (SYS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).

Interpretation:

- For the mean density of 1 individual/cell at high aggregation levels, all variance estimators yield low coverage ratio values, and the situation is similar for the three sampling methods, excepted for the largest sample sizes ($n = 196$ and 400). This is probably due to the high proportion of zeros in the samples for these populations, e.g. for the populations with a mean density of 1 individual/cell and a dispersion index of $I = 60$, the samples contained on average 97% of zeros, with very little difference between the three sampling methods. For the same level of dispersion index, the proportion of zeros in the samples drops to 76% and 60% for the mean densities of 10 and 20 individuals/cell respectively.
- Leaving aside the populations with mean density of 1 individual/cell and the sample size of $n = 9$, the coverage ratio values are around 0.95 for all the estimators that provided unbiased or overestimated estimates of the sampling variance, and below 0.95 for the estimators that tended to underestimate variance, i.e. V_{8} , V_{w} and V_{ZIP} for SYS, and V_{nbh} and V_{ZIP} for SBS.

1.3 Comparison of the estimated variance for SYS and SBS to the estimated variance for SRS

In this section, we represent the ratio of the variance estimated using the variance estimators for SYS and SBS over the variance estimated using the “textbook” estimator for SRS. When this ratio is below one, it means that using SYS or SBS with a given estimator yields more precise estimates than using SRS with V_{textbook} , and when it’s above one, it’s the opposite. The interpretation is difficult here, as several estimators present biased estimates at least for some density and aggregation levels.



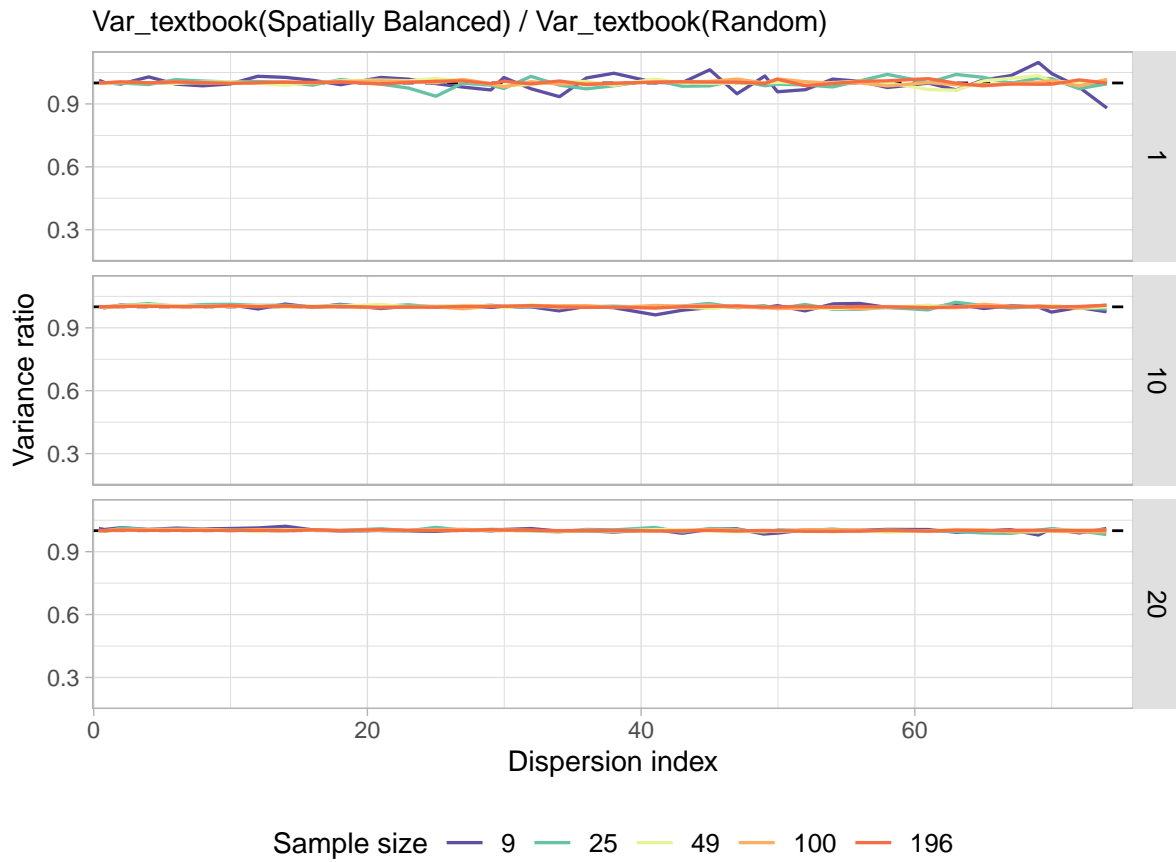
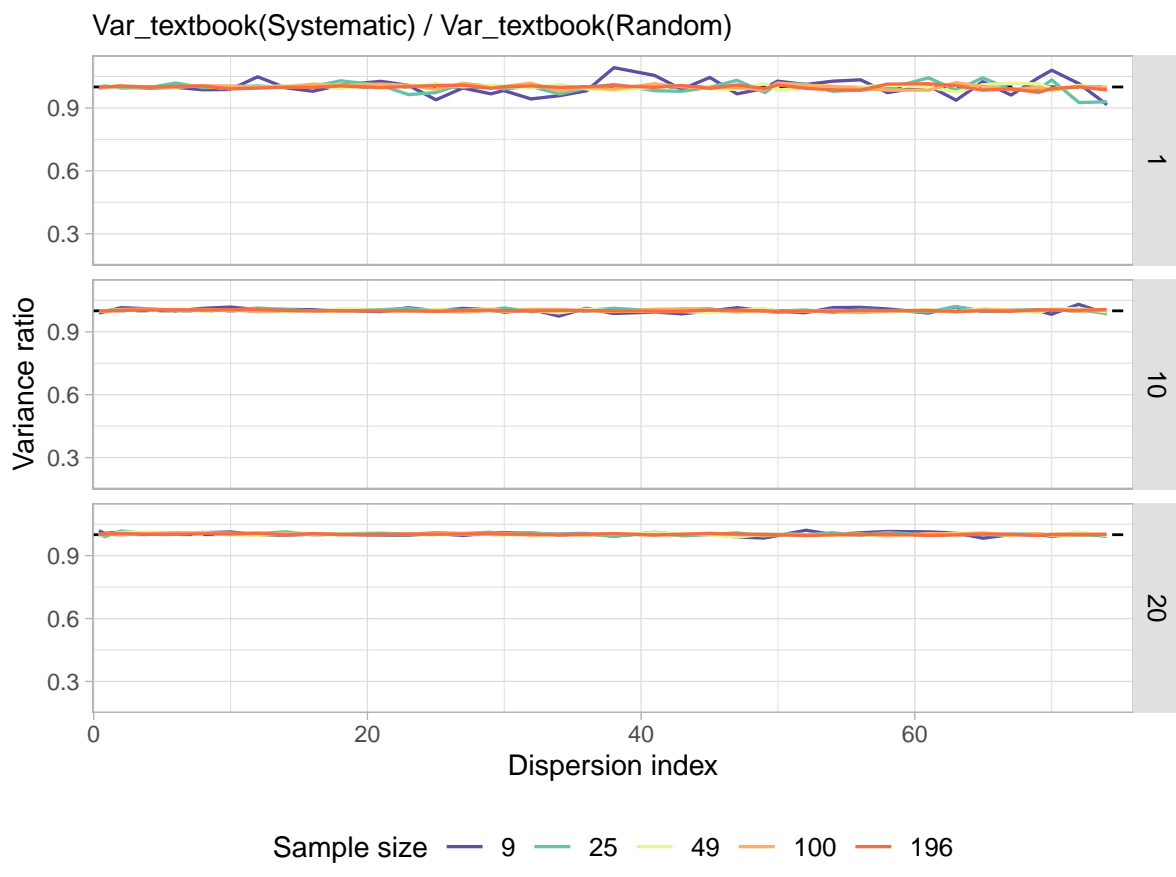
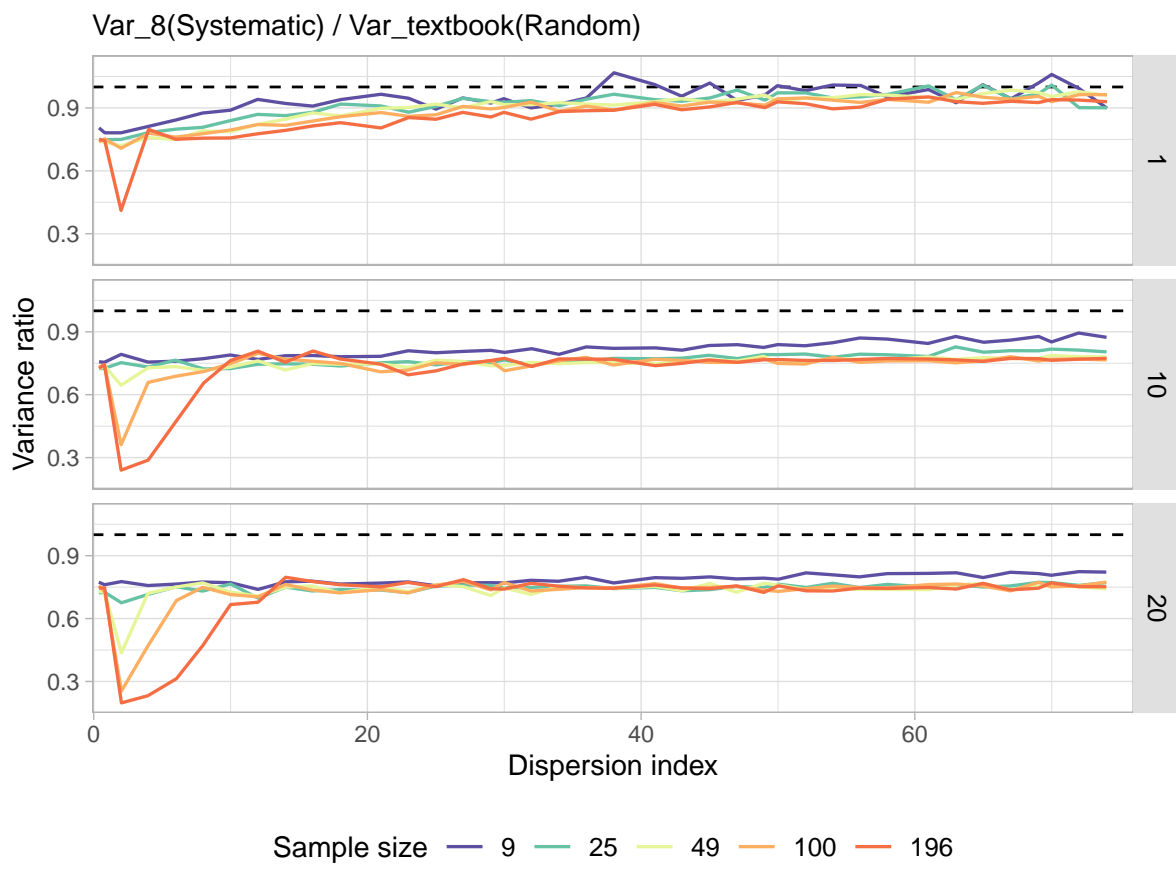
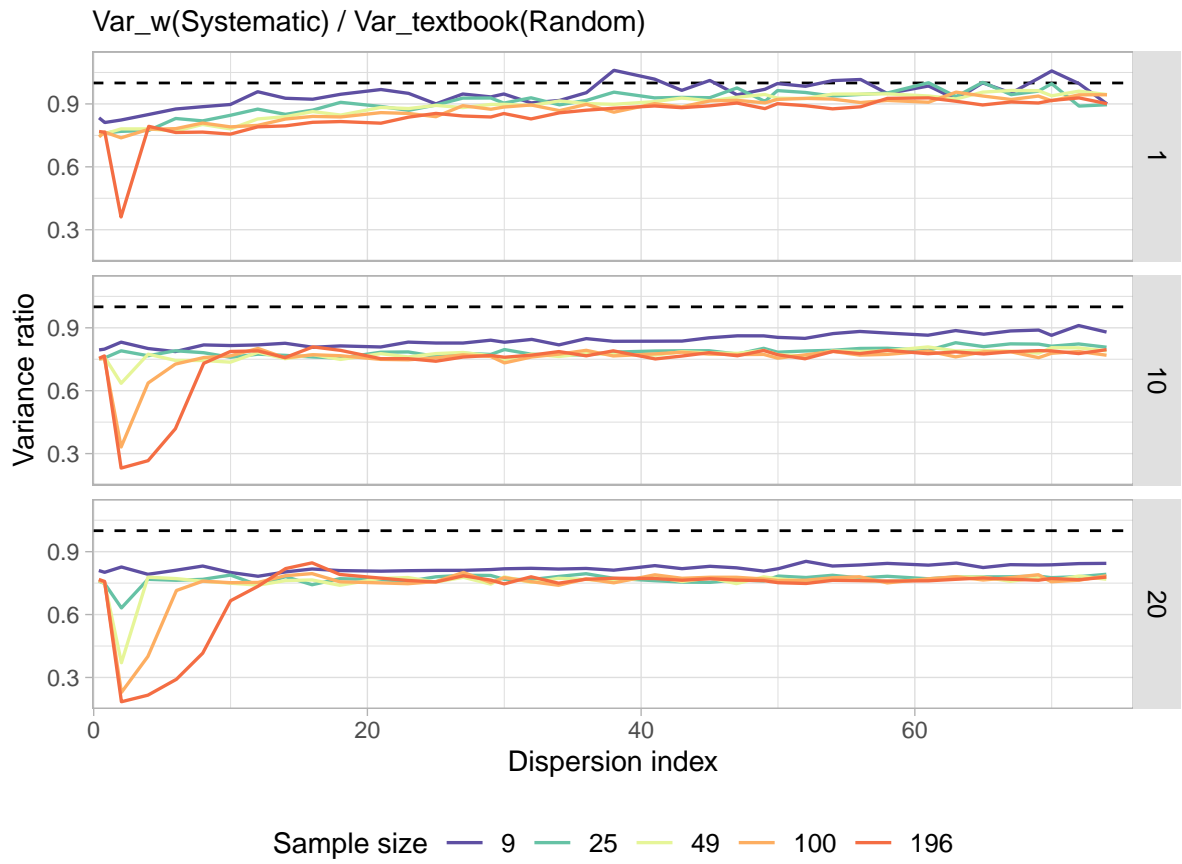
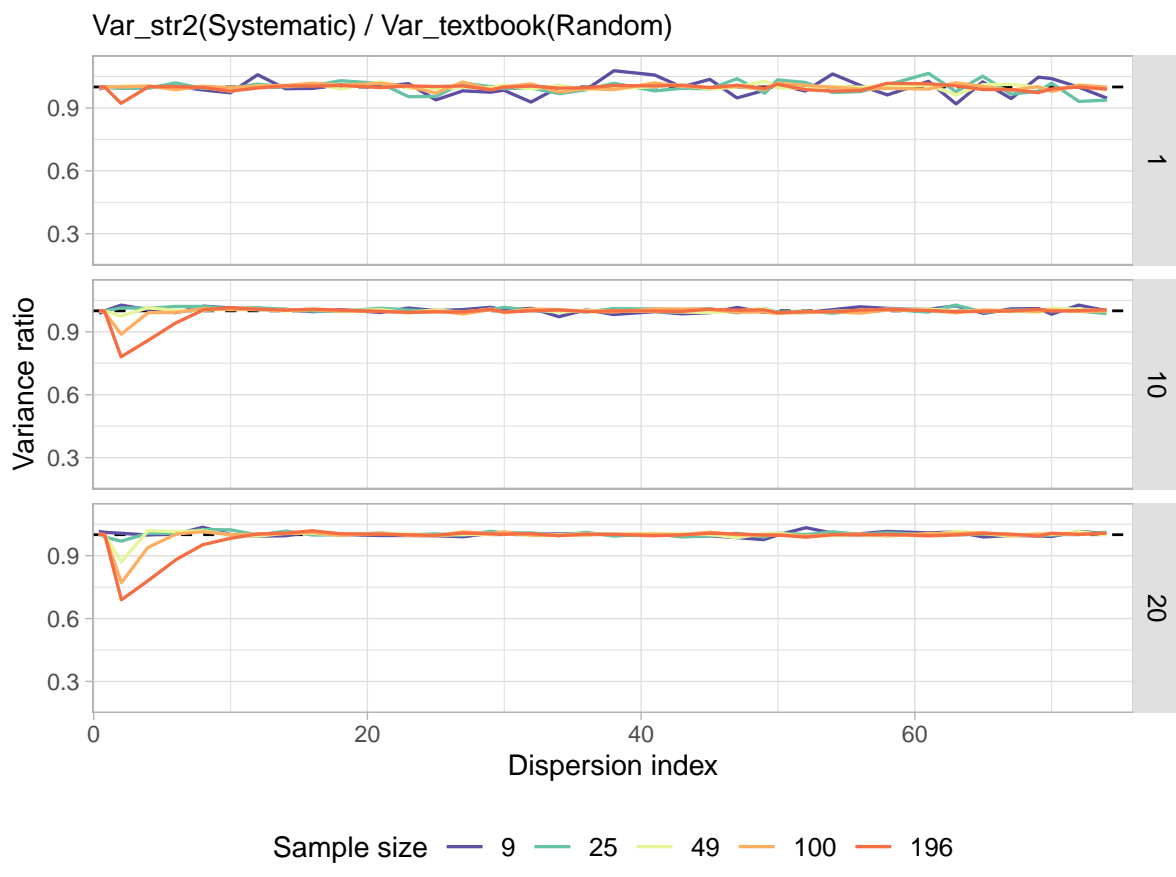


Figure S4.7: Ratio of the variance estimated using the “textbook” estimator for systematic sampling (SYS) and spatially balanced sampling (SBS) over the variance estimated for simple random sampling (SRS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).









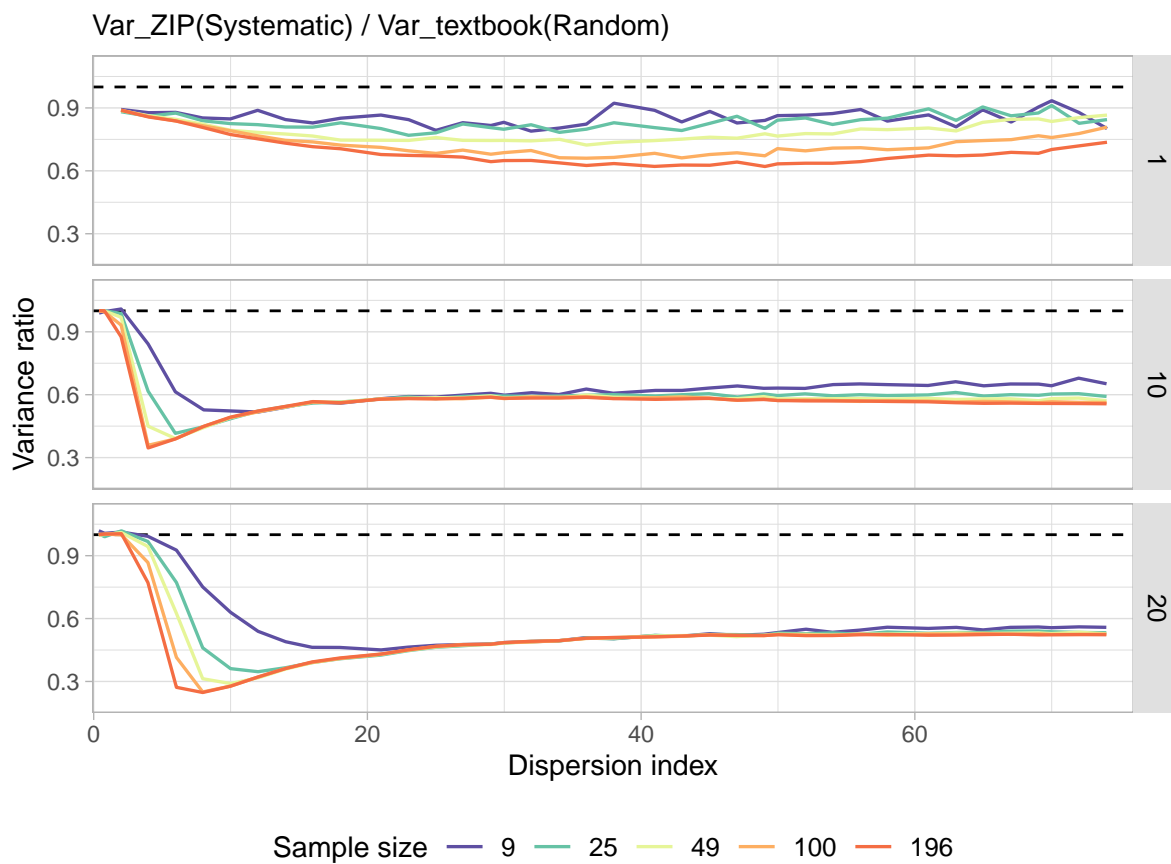
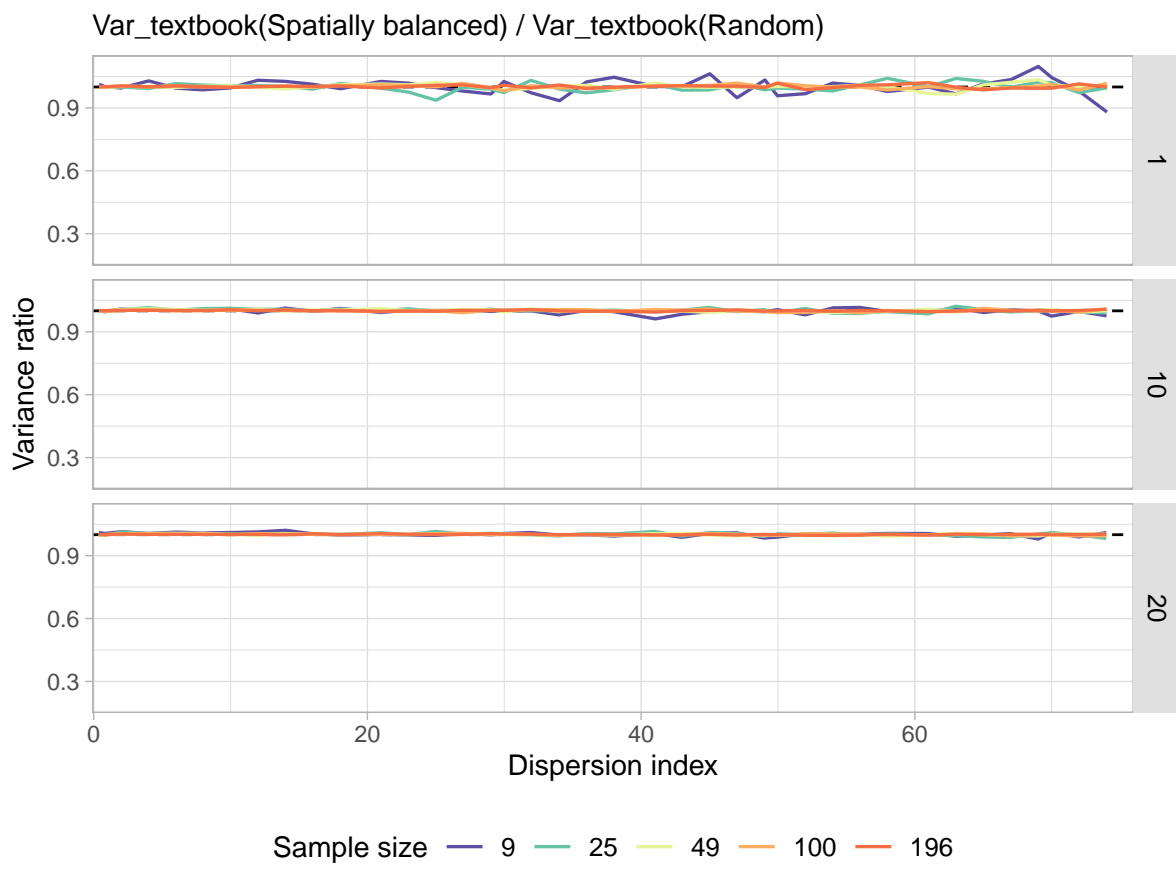
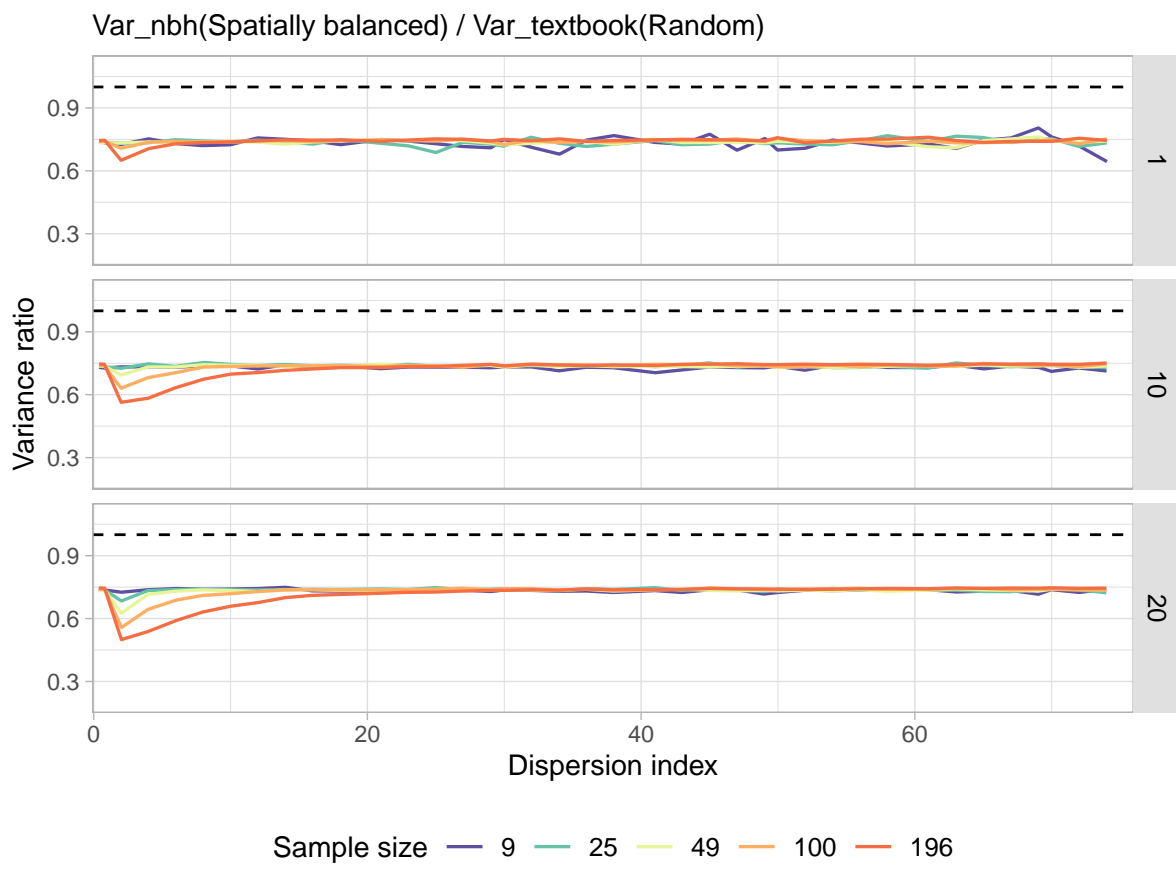


Figure S4.8: Ratio of the variance estimated using five variance estimators (V_{textbook} , V_8 , V_w , V_{str2} , V_{ZIP}) for systematic sampling (SYS) over the variance estimated using the “textbook” estimator for simple random sampling (SRS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).





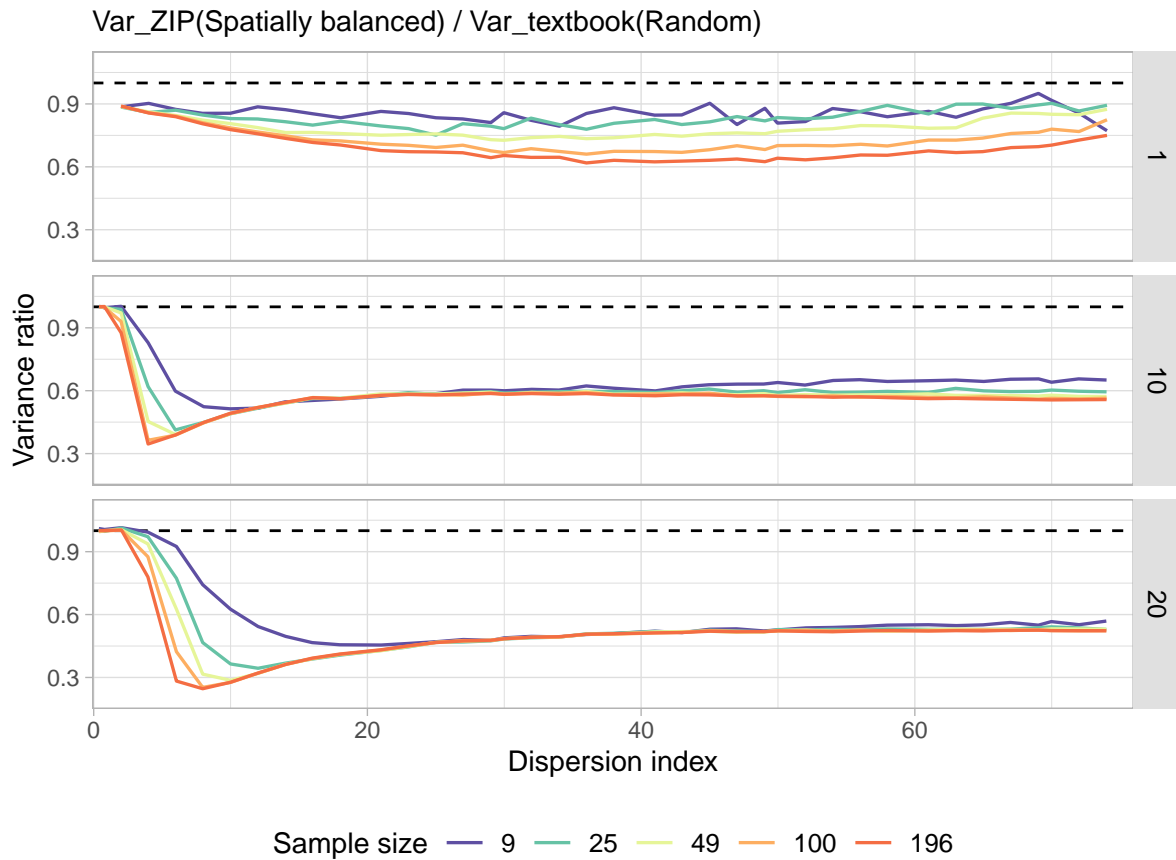


Figure S4.9: Ratio of the variance estimated using three variance estimators (V_{textbook} , V_{nbh} and V_{ZIP}) for spatially balanced sampling (SYS) over the variance estimated using the “textbook” estimator for simple random sampling (SRS), as a function of the dispersion index (I) of the sampled populations. Panels show three different mean densities of individuals (1, 10 and 20 individuals/cell).

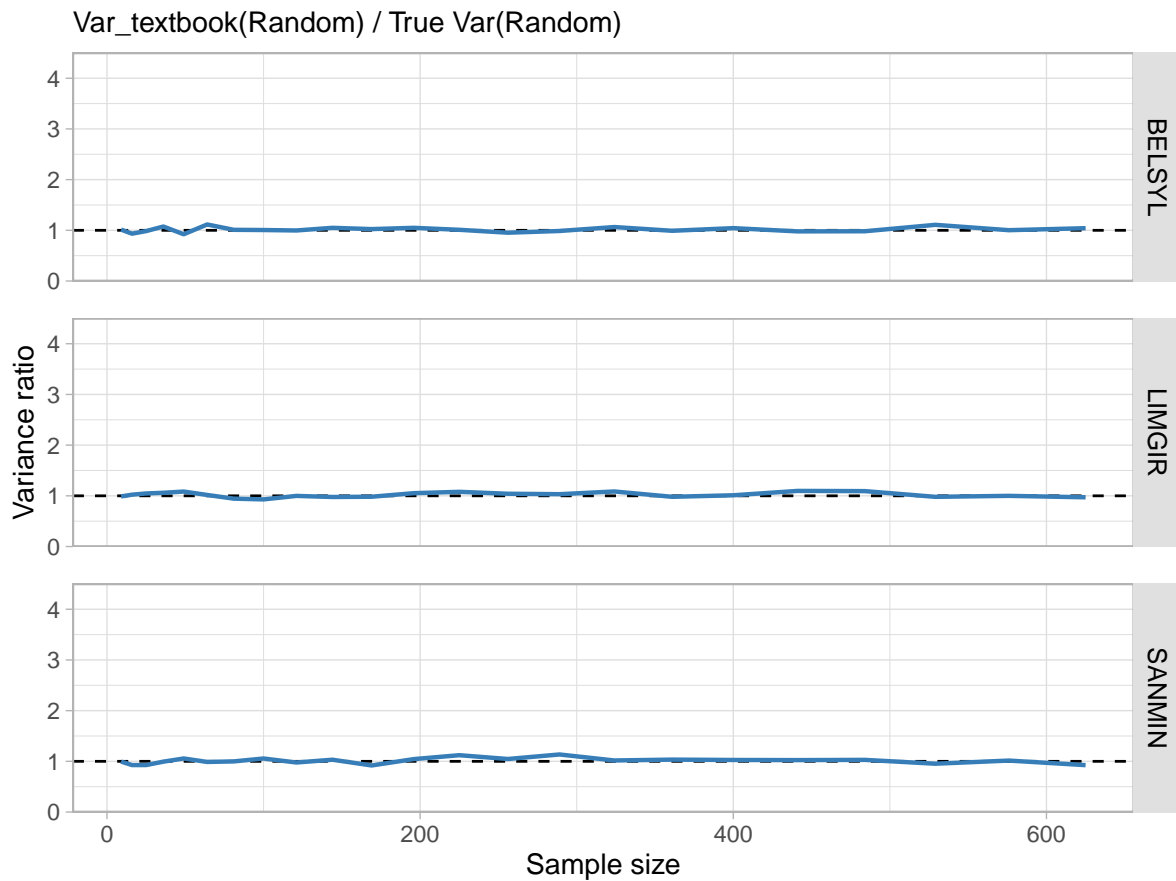
Interpretation:

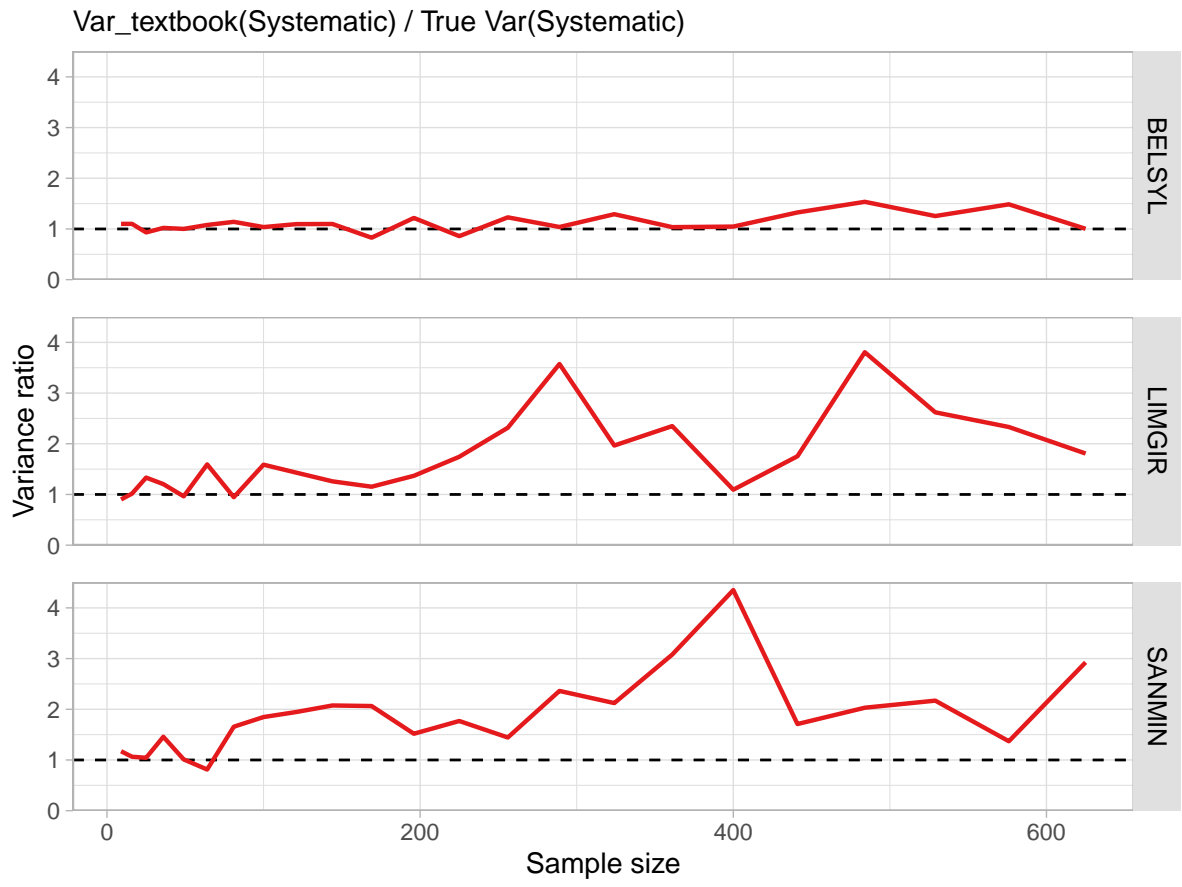
- For the aggregation levels where SYS and SBS provide the greatest increase in precision relative to SRS, when using the estimators based on the correlation of abundance among neighbouring units, a gain in precision is on average observed despite the fact that these estimators all tend to overestimate the variance.
- Under these conditions, the V_{ZIP} estimator allows for the highest gain in apparent accuracy, for both SYS and SBS.
- Leaving aside these levels of aggregation, using SYS and the estimators V_8 , V_w or V_{ZIP} , and using SBS and the estimators V_{nbh} or V_{ZIP} seem to allow a consistent increase in the observed precision compared to using SRS and the textbook estimator, but this is mostly due to the estimators underestimating the sampling variance, as for these aggregation levels there is almost no difference in true variance between the sampling methods (Fig. 2).
- The tendency of V_8 and V_w to underestimate sampling variance for SYS was expected given that we simulated aggregated populations using the Matern process. Indeed, for the high levels of aggregation the populations are composed of clusters with a diameter smaller than the distance between the sampling units, and the clusters are randomly located across the study area. Thus the average correlation of abundance among neighbouring units will be around zero, with an equal chance of being positive or negative. But the V_8 and V_w formulas specify that no correction is made to the textbook estimator when the average correlation between neighbouring units is negative, which certainly leads to this

tendency to underestimate the sampling variance on average. See McGarvey et al. (2016) pages 245-246 for a more detailed discussion on this topic.

2. Natural populations

2.1 Comparison of estimated variance and true variance





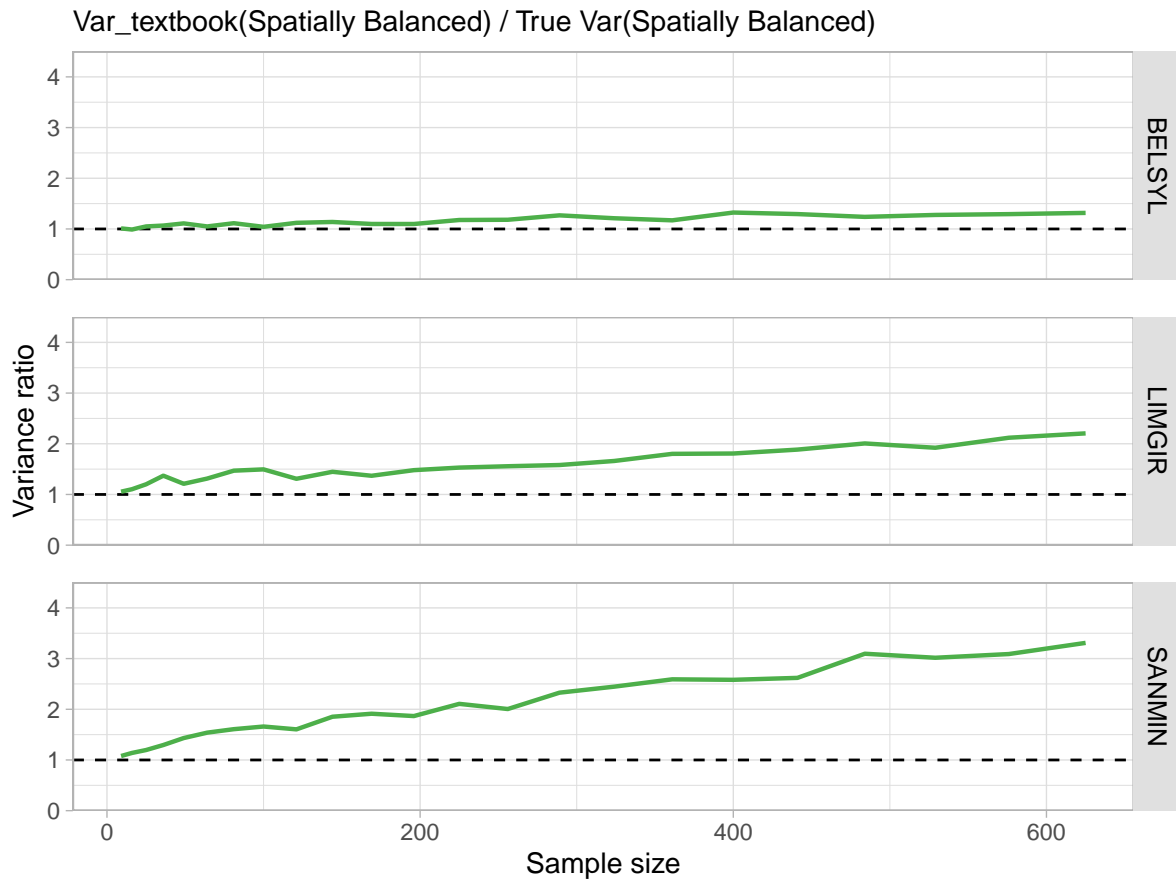
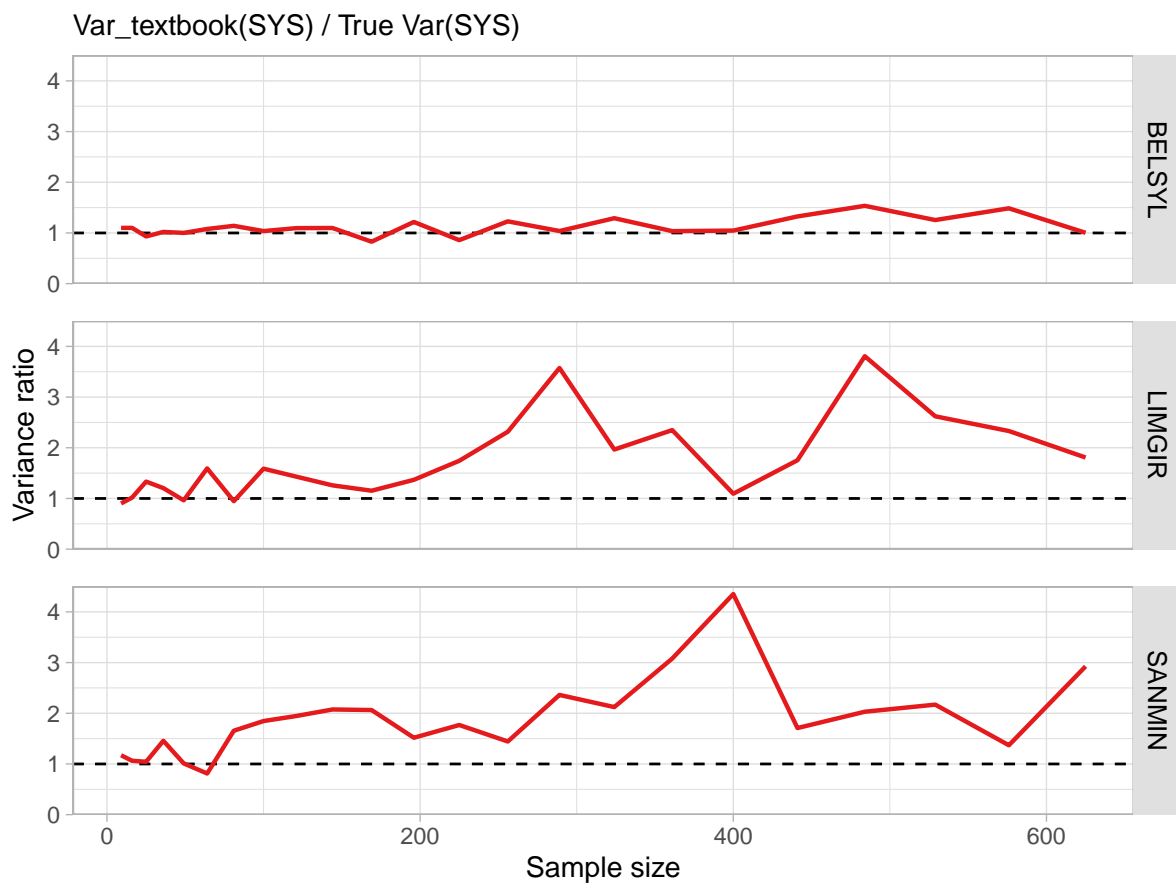
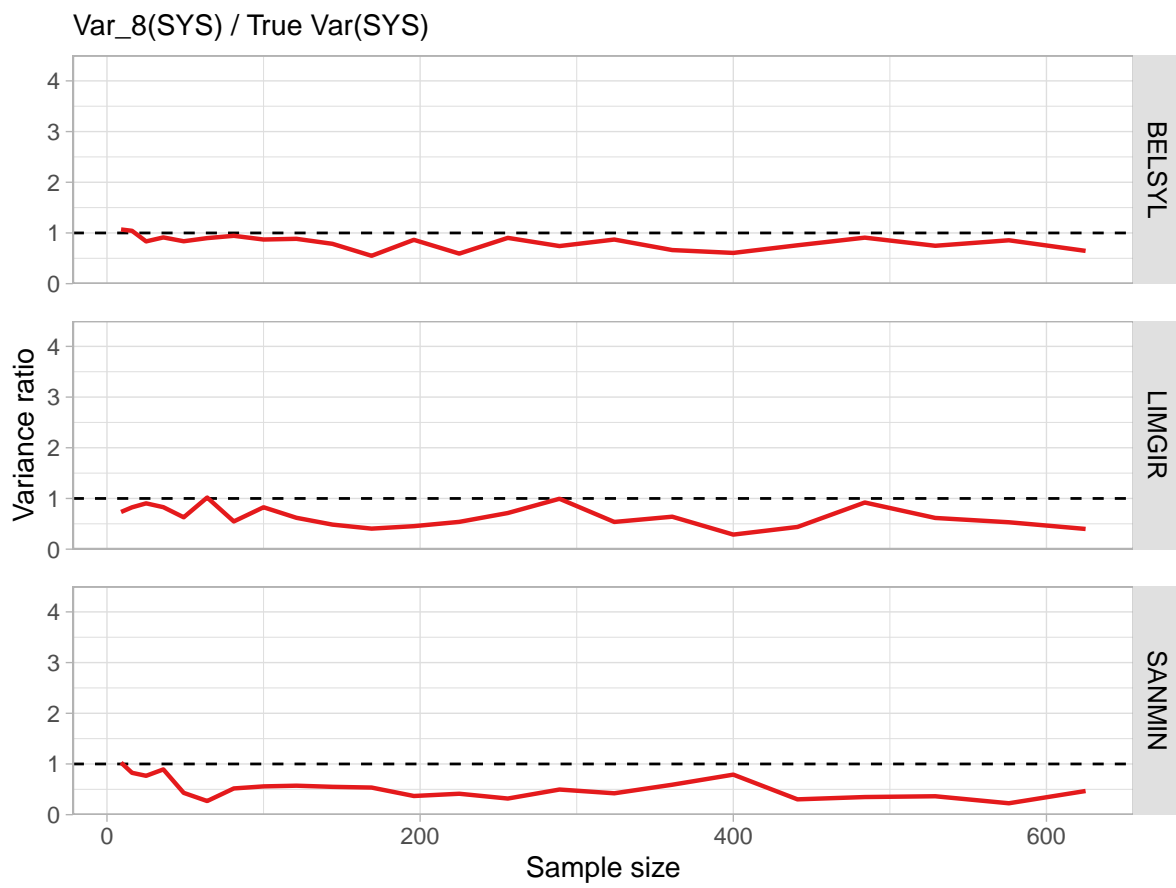
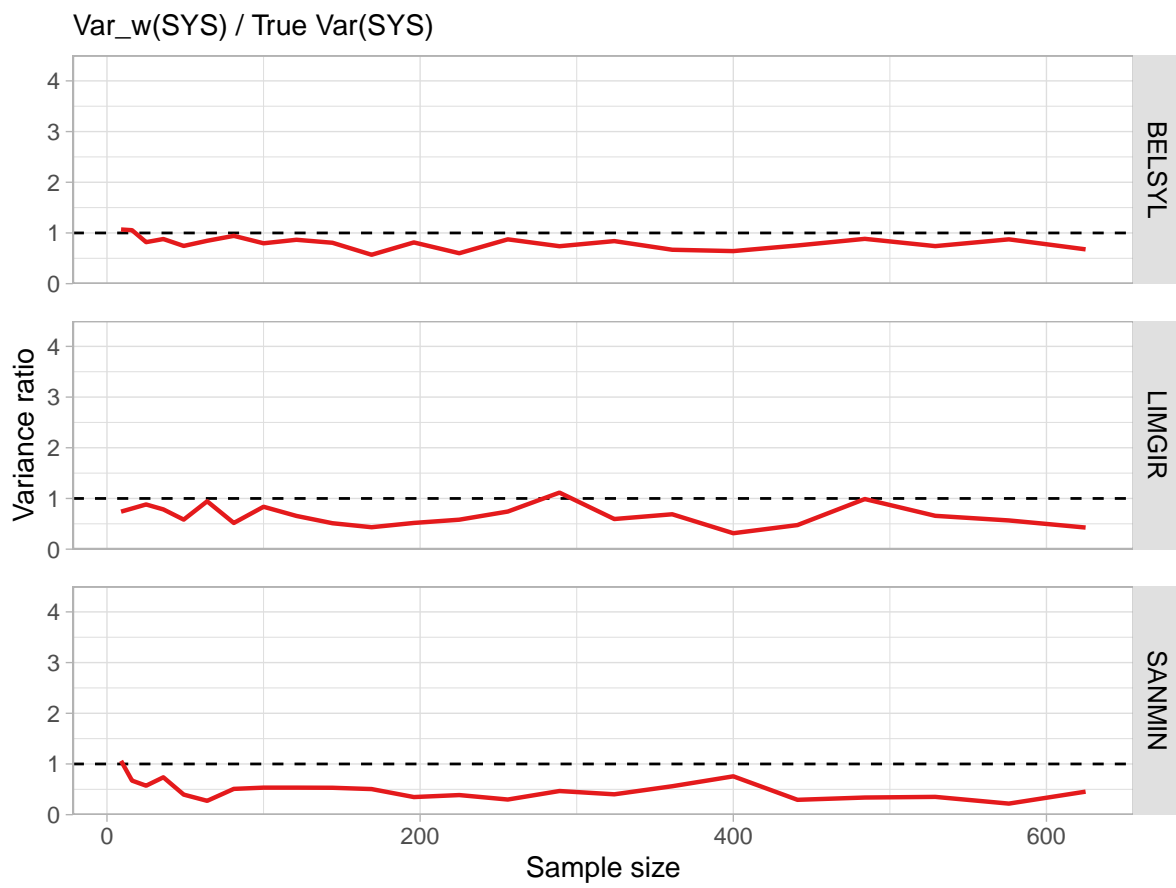
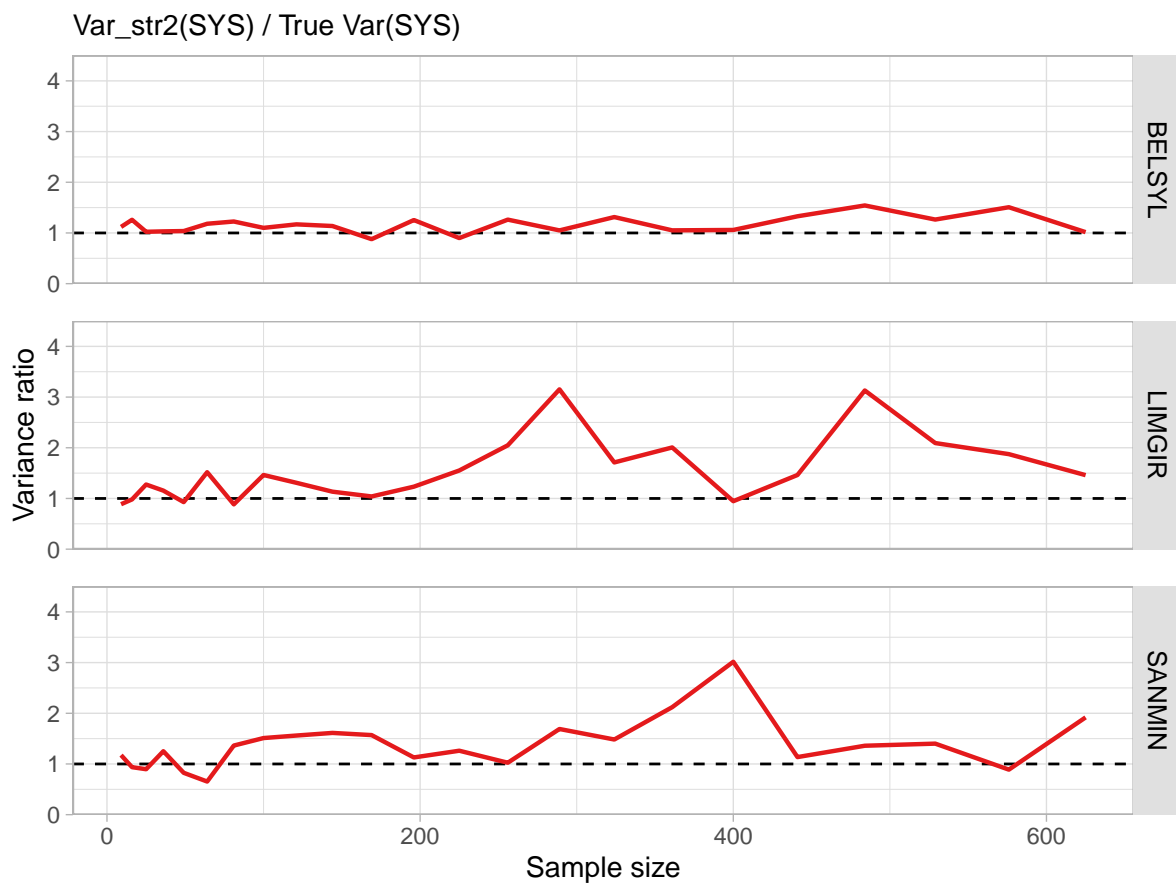


Figure S4.10: Ratio of the estimated sampling variance using the “textbook” estimator over the true sampling variance for simple random sampling (SRS), systematic sampling (SYS) and spatially balanced sampling (SBS), as a function of sample size for the three natural populations. As expected from sampling theory, using the “textbook” estimator for SYS and SBS leads to a strong overestimation of the sampling variance.









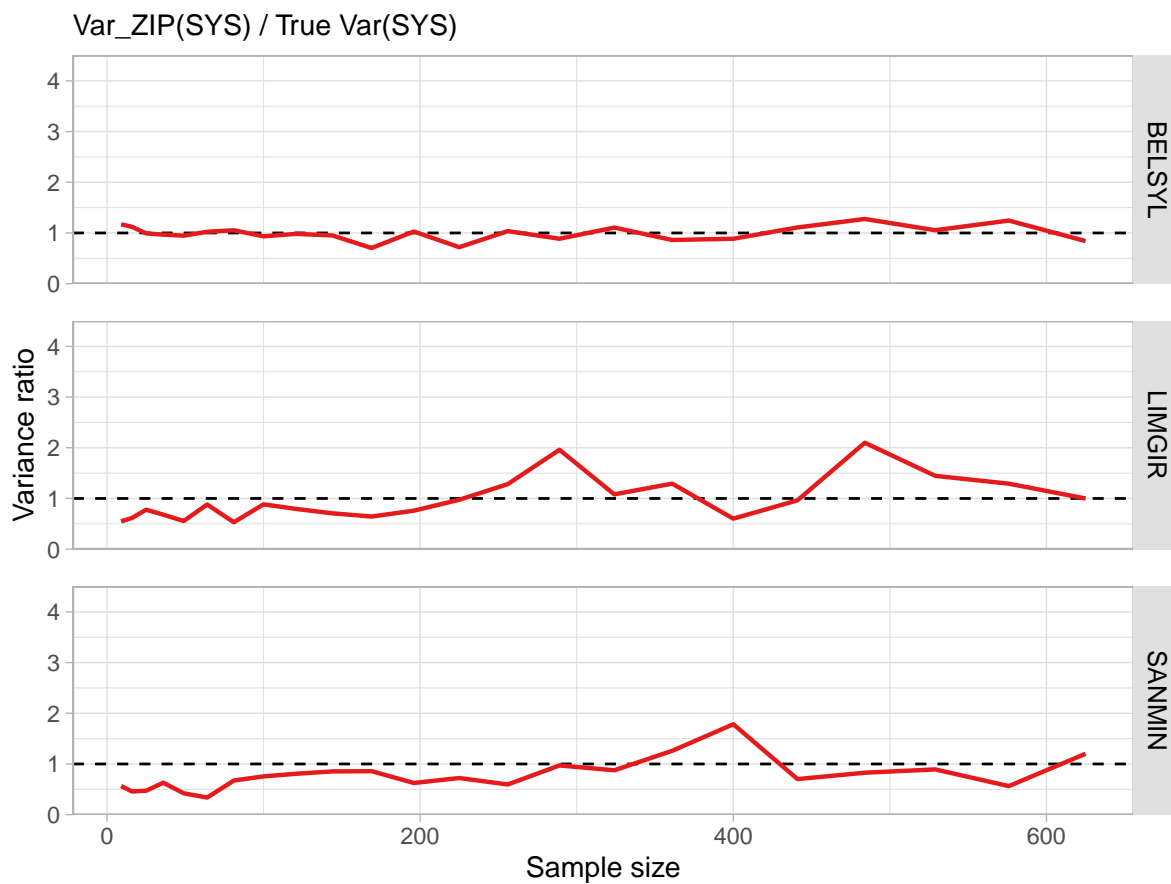
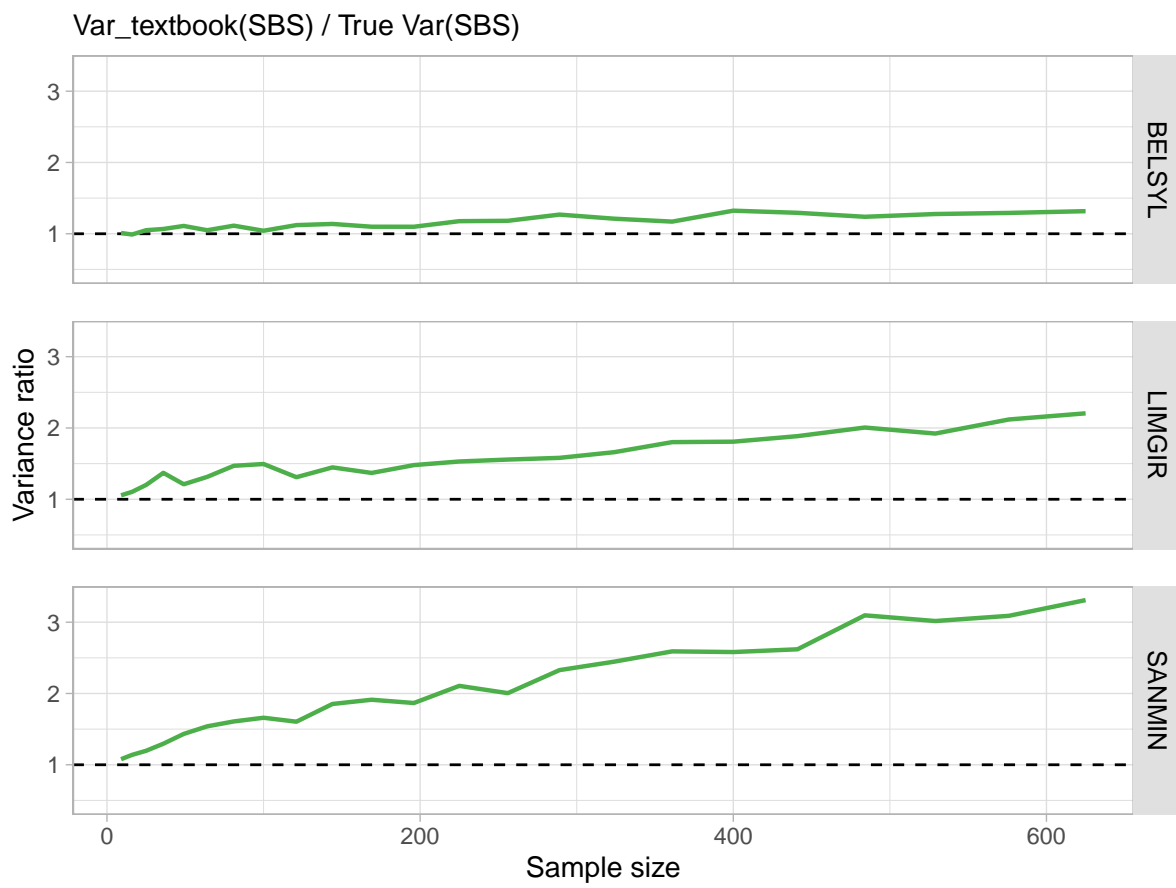
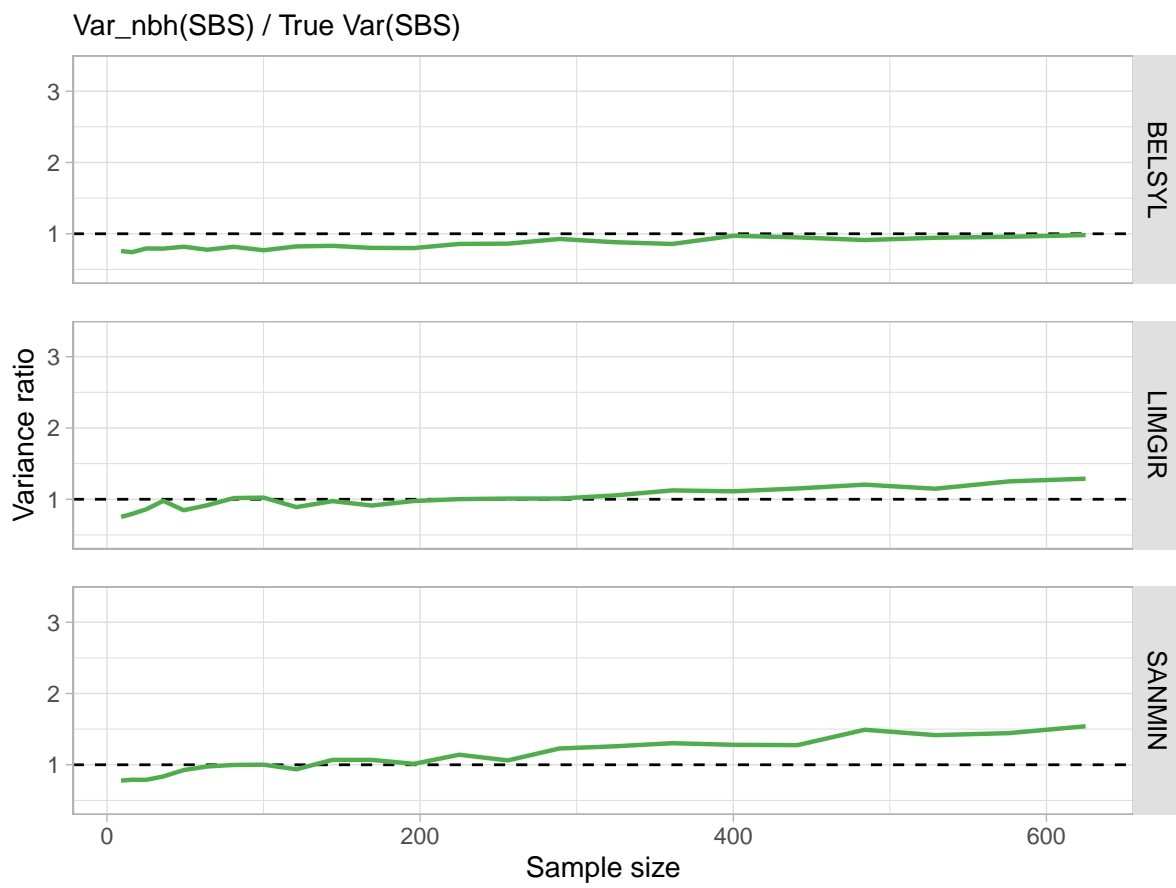


Figure S4.11: Ratio of the estimated sampling variance using five variance estimators (V_{textbook} , V_8 , V_w , $V_{\text{str}2}$, V_{ZIP}) over the true sampling variance for systematic sampling (SYS), as a function of sample size for the three natural populations.





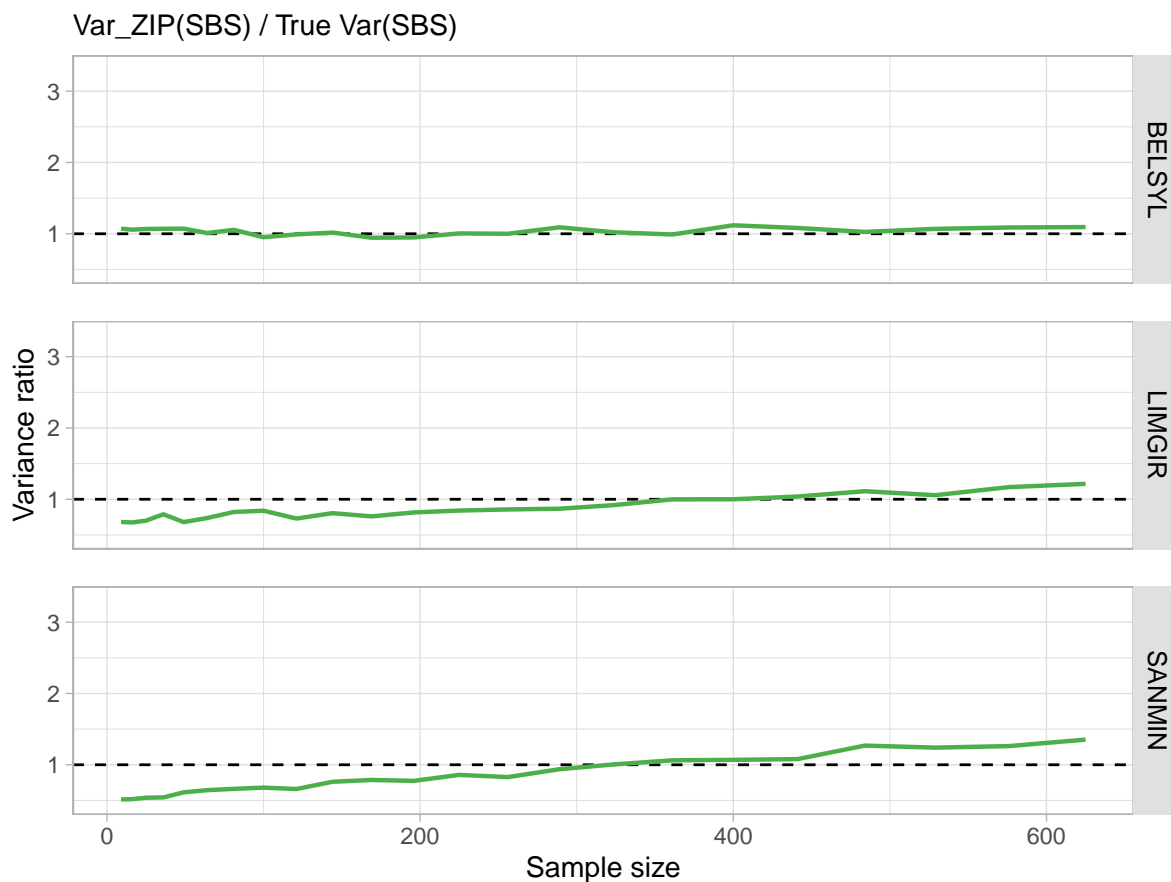
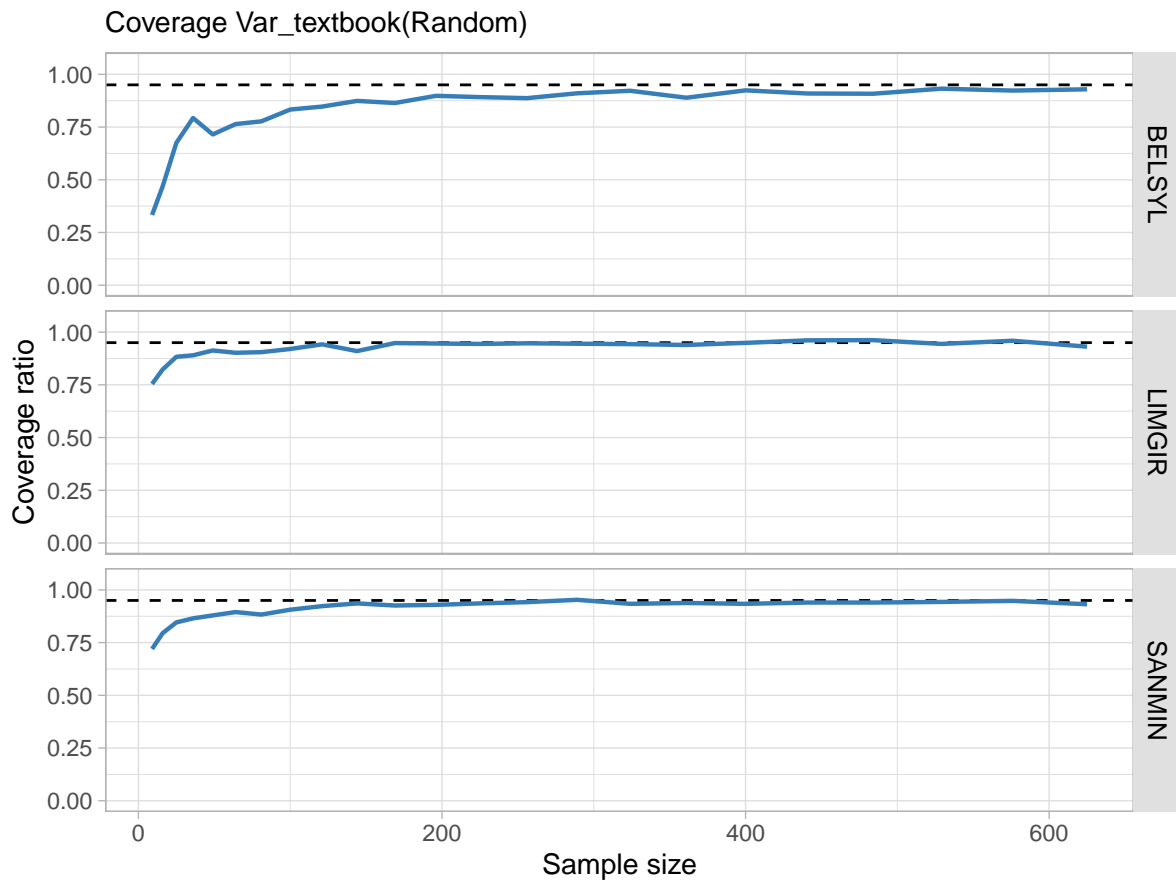


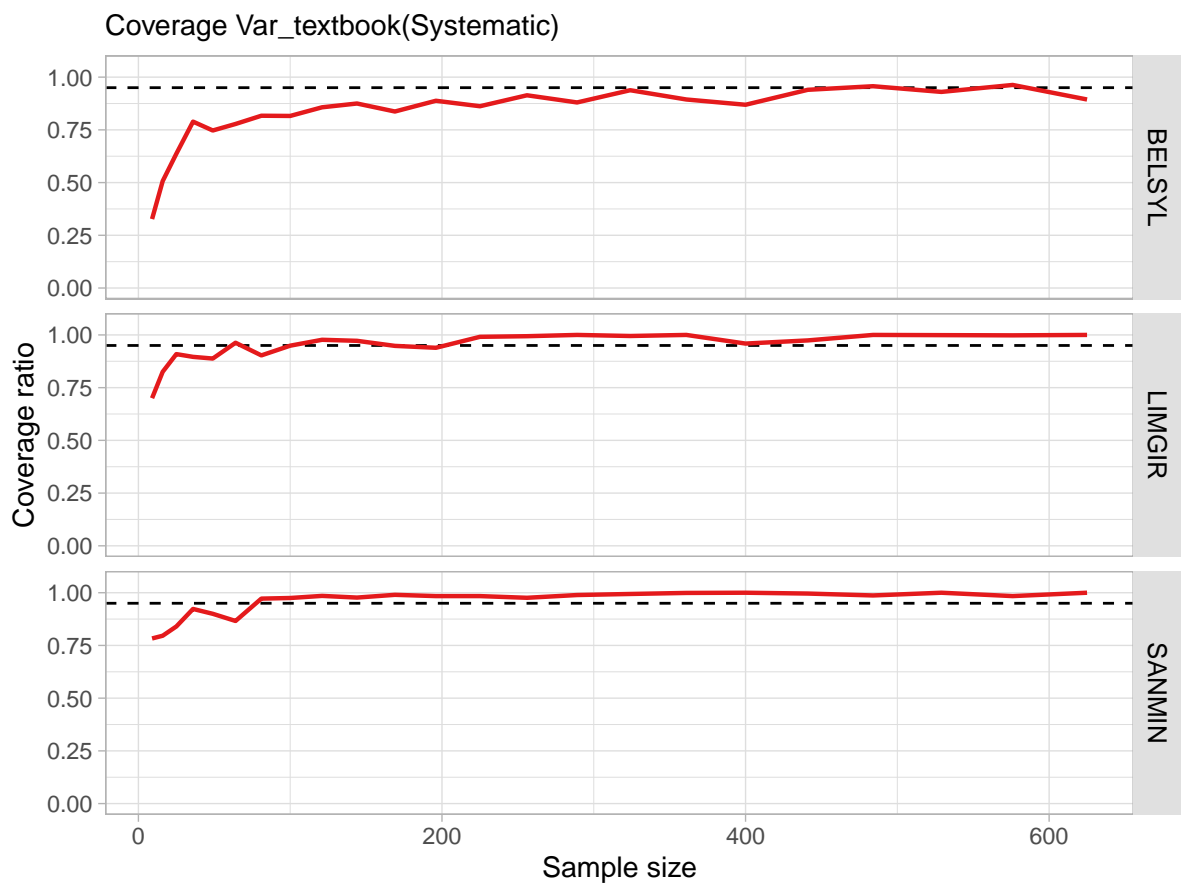
Figure S4.12: Ratio of the estimated sampling variance using three variance estimators (V_{textbook} , V_{nbh} and V_{ZIP}) over the true sampling variance for spatially balanced sampling (SYS), as a function of sample size for the three natural populations.

Interpretation:

- For the population of *Bellis sylvestris* (BELSYL) there is little difference in true sampling variance between the three sampling methods (Fig. 4), and the textbook estimator provides nearly unbiased estimates for SYS and SBS. For the other two populations, V_{textbook} substantially overestimates the sampling variance (Fig. S4.10).
- For SYS, V_8 and V_w tend to underestimate the sampling variance as for the virtual populations. The estimates obtained with V_{str2} are unbiased or overestimated, but less overestimated than V_{textbook} . V_{ZIP} tends to underestimate sampling variance, but less than V_8 and V_w .
- For SBS, V_{nbh} provides nearly unbiased estimates despite a tendency to overestimation for larger sample sizes. The V_{ZIP} estimator also performs fairly well, but less than V_{nbh} .

2.2 Estimator coverage ratio





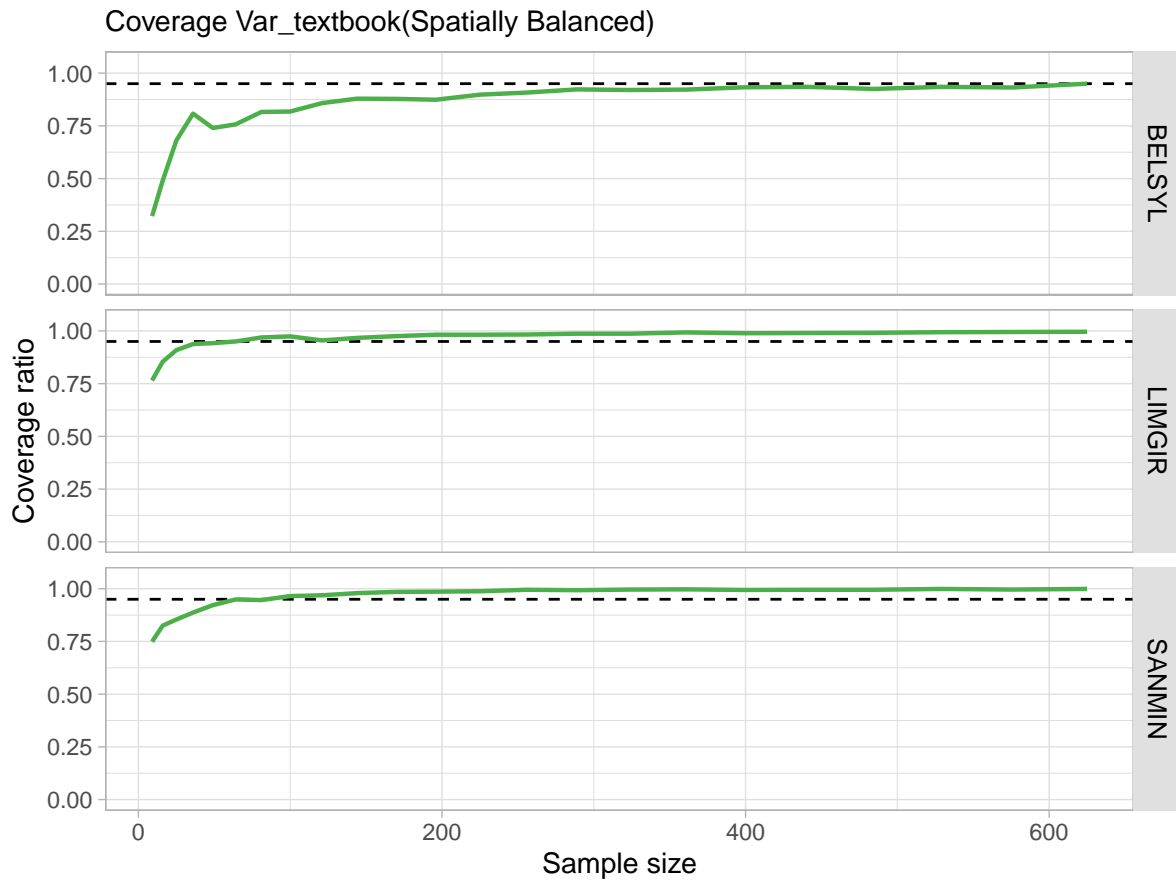
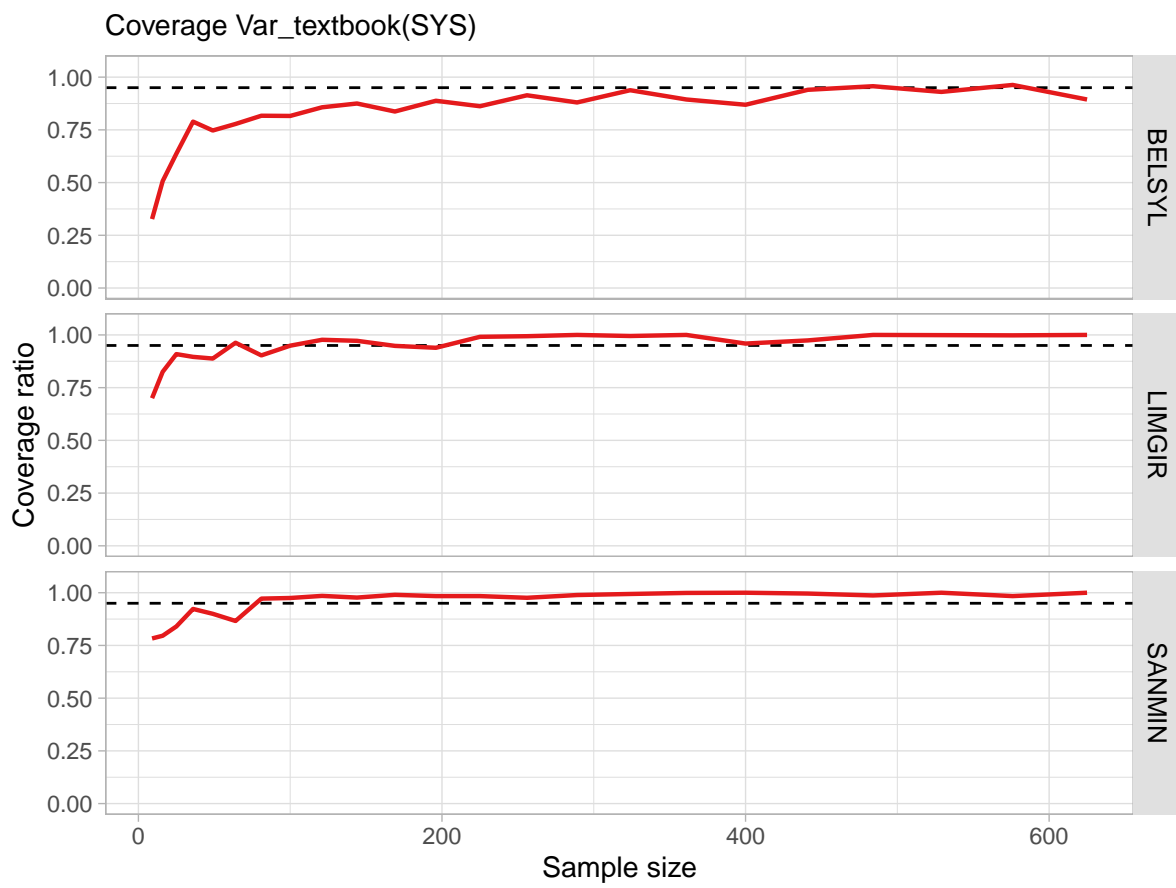
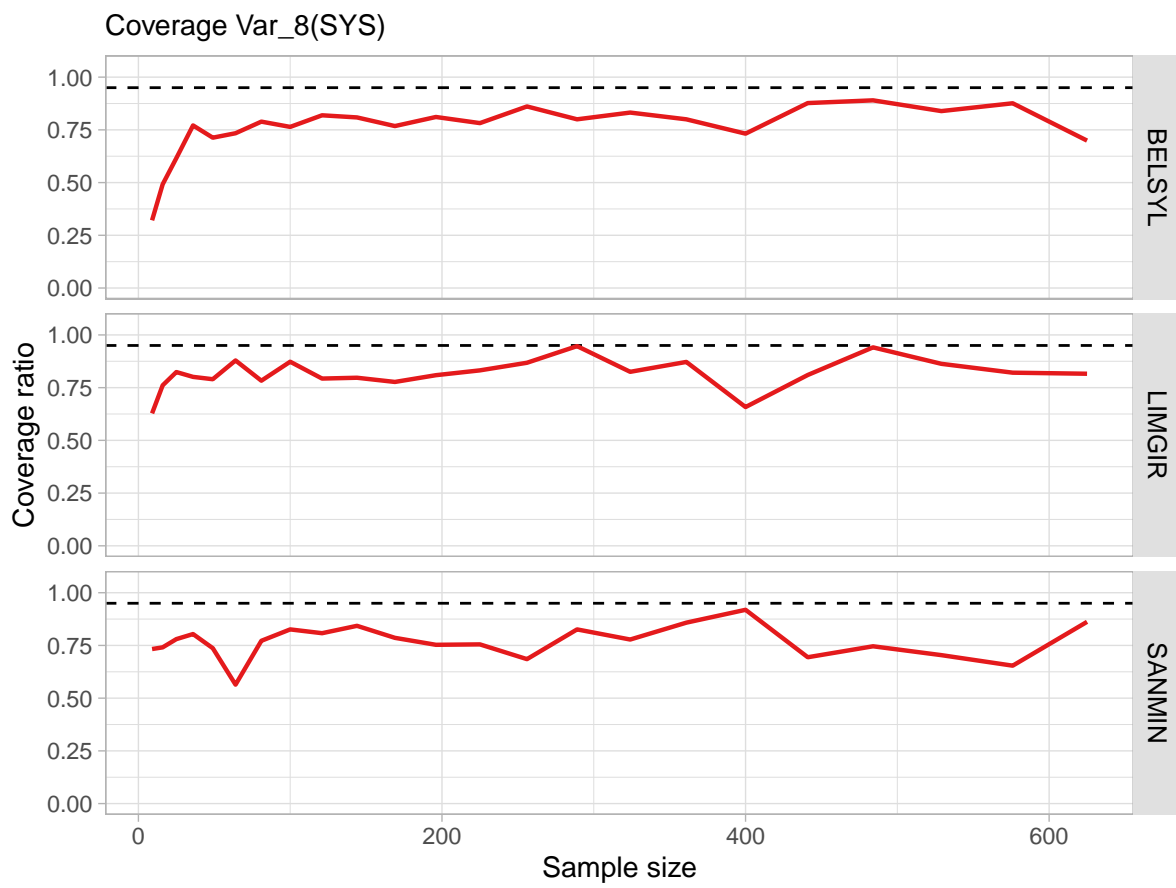
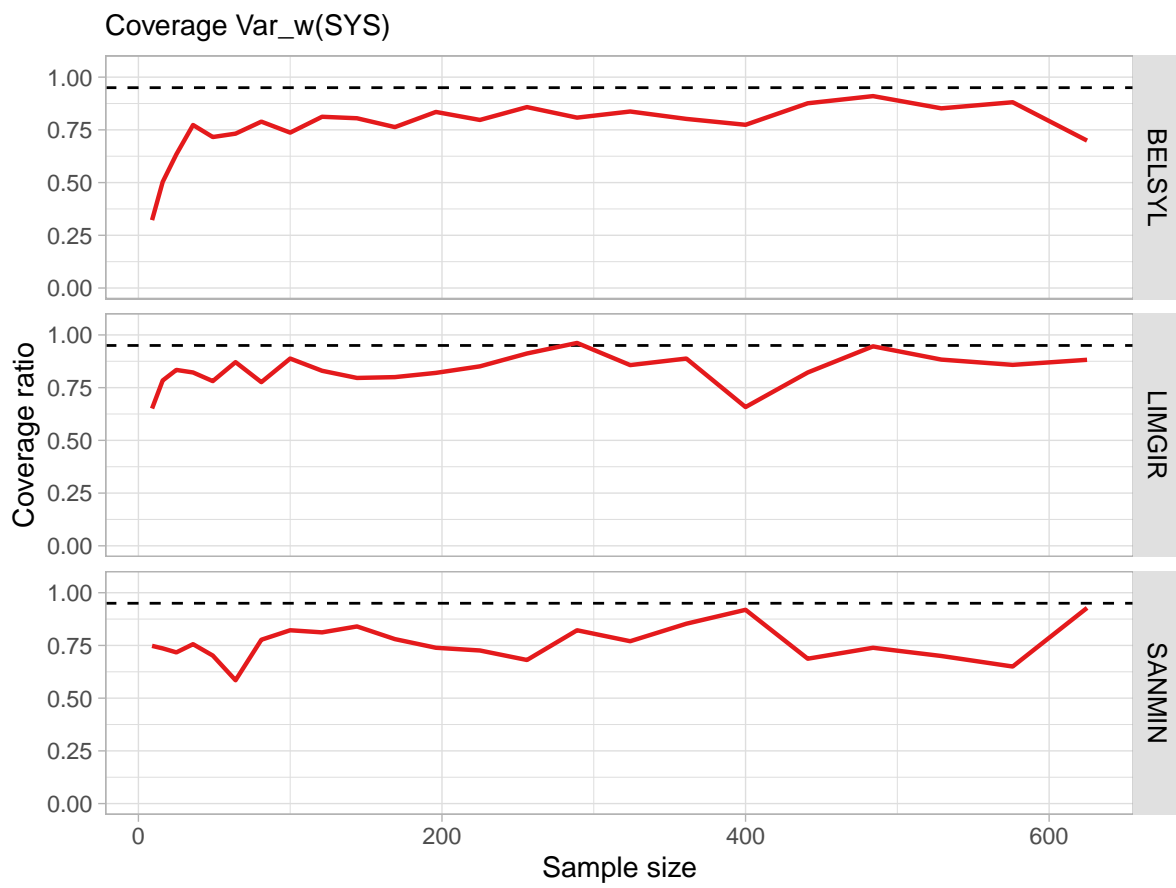
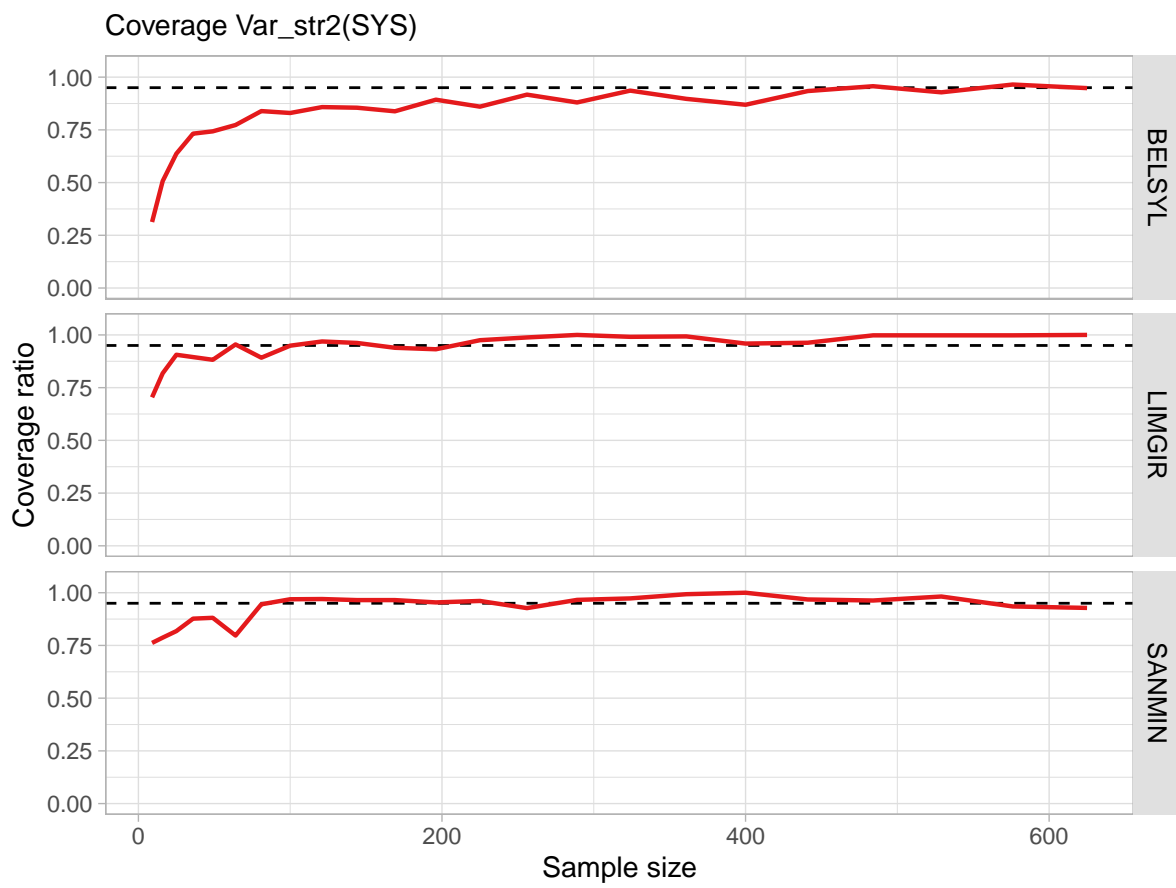


Figure S4.13: Coverage ratio of the “textbook” estimator for simple random sampling (SRS), systematic sampling (SYS) and spatially balanced sampling (SBS), as a function of sample size for the three natural populations.









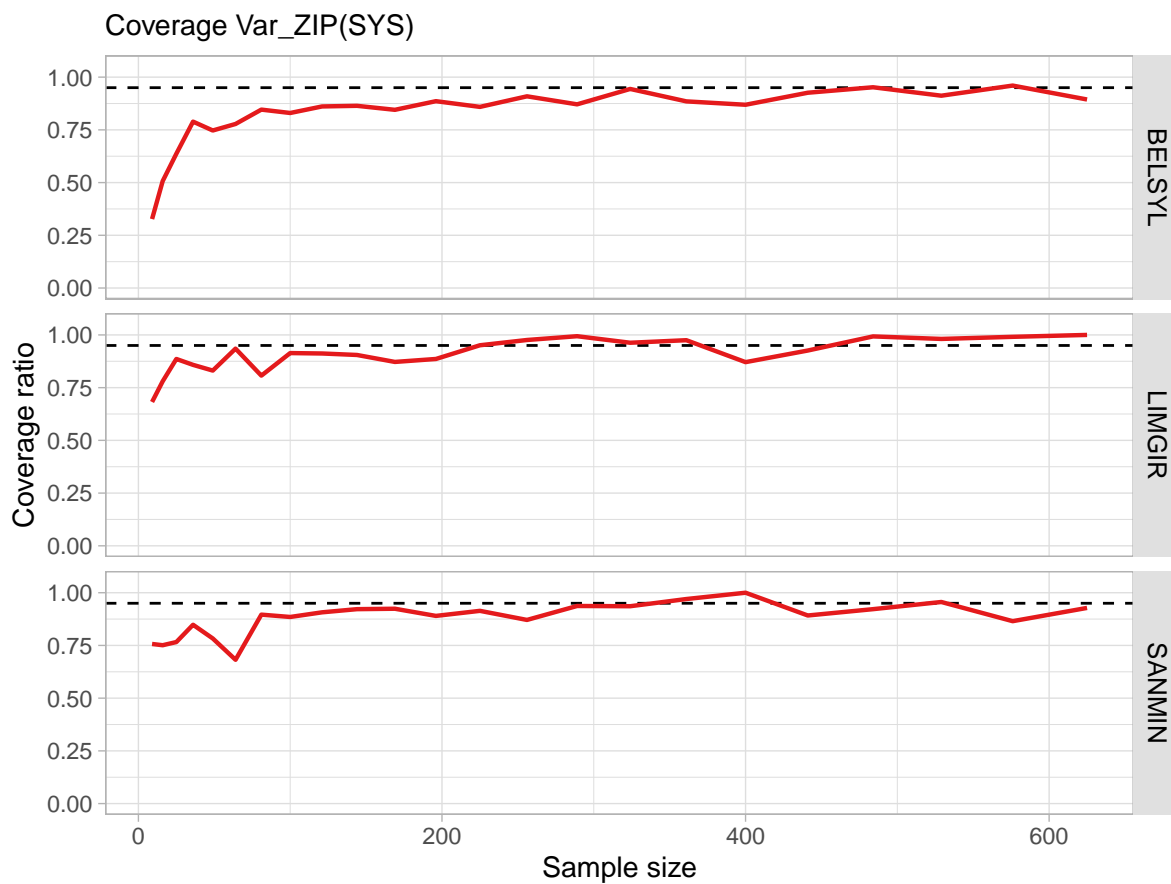
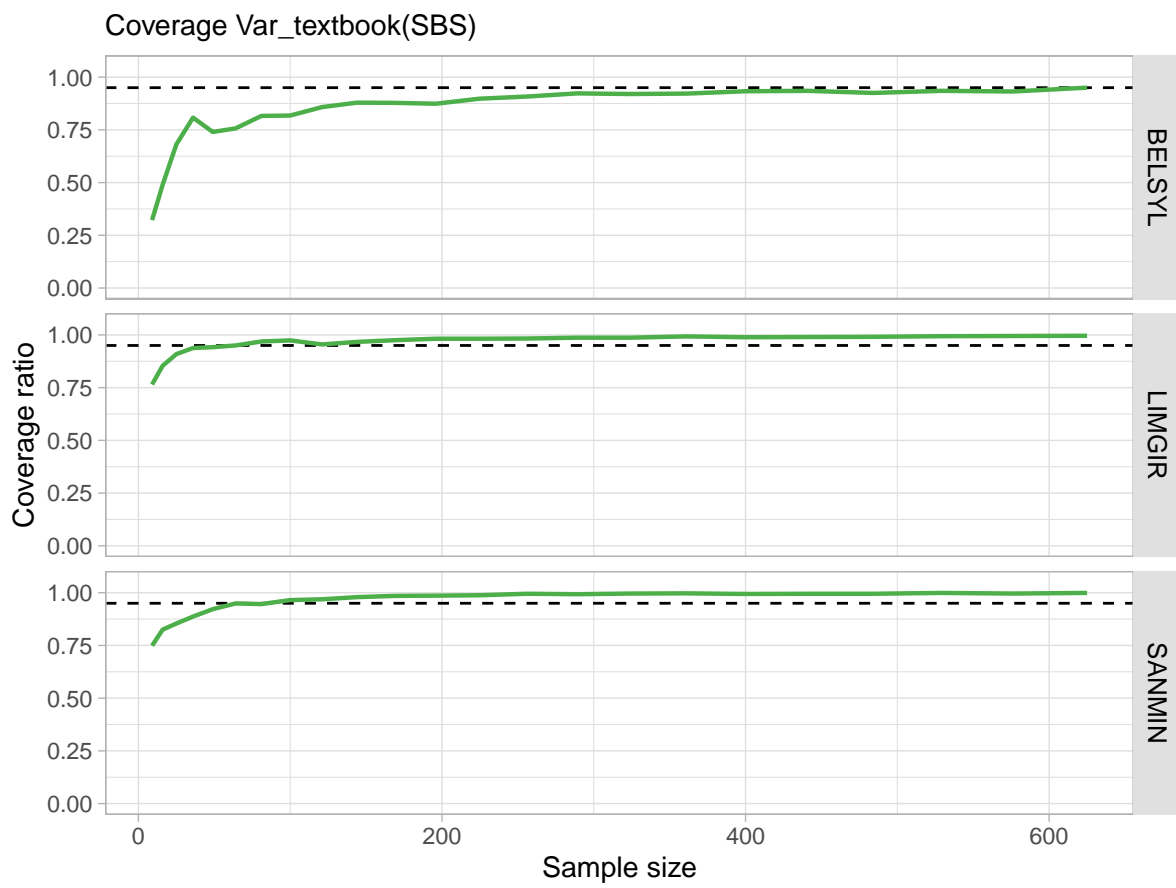
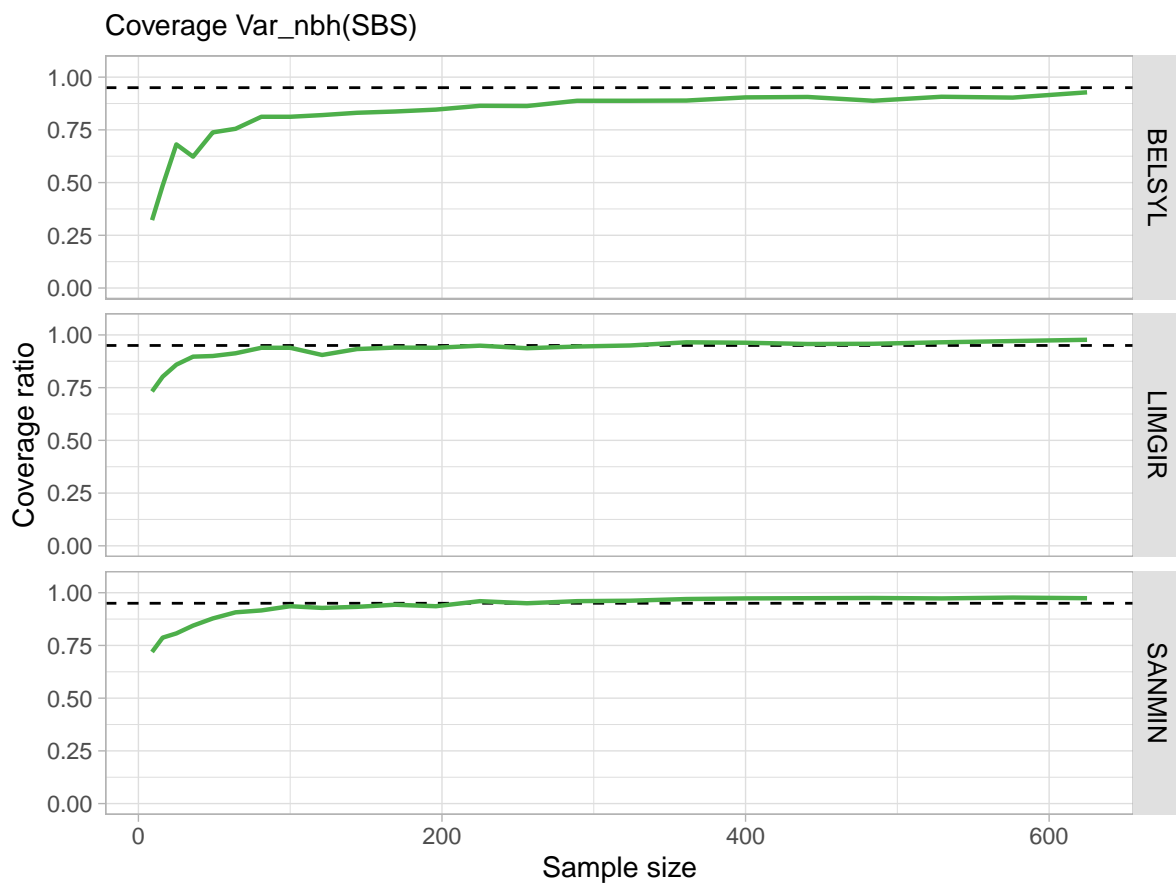


Figure S4.14: Coverage ratio of five variance estimators (V_{textbook} , V_8 , V_w , V_{str2} , V_{ZIP}) for systematic sampling (SYS), as a function of sample size for the three natural populations.





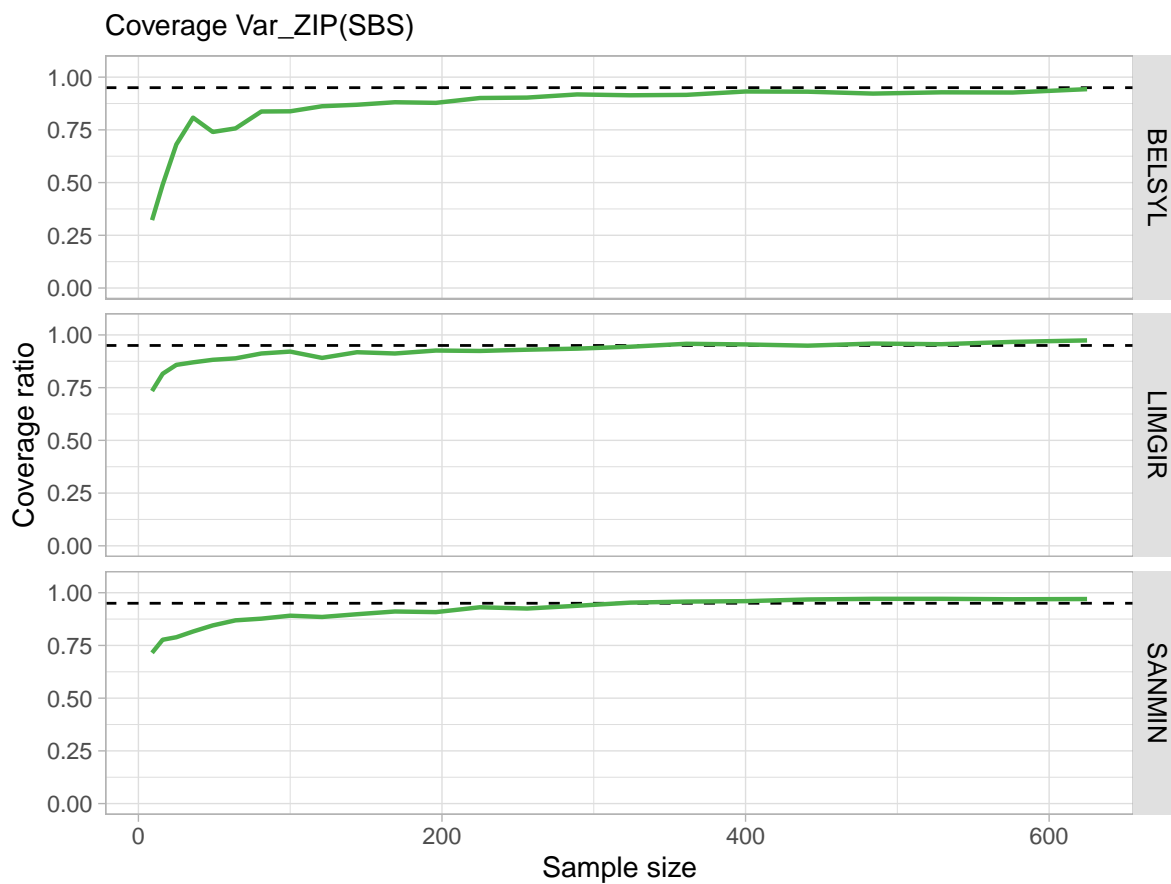
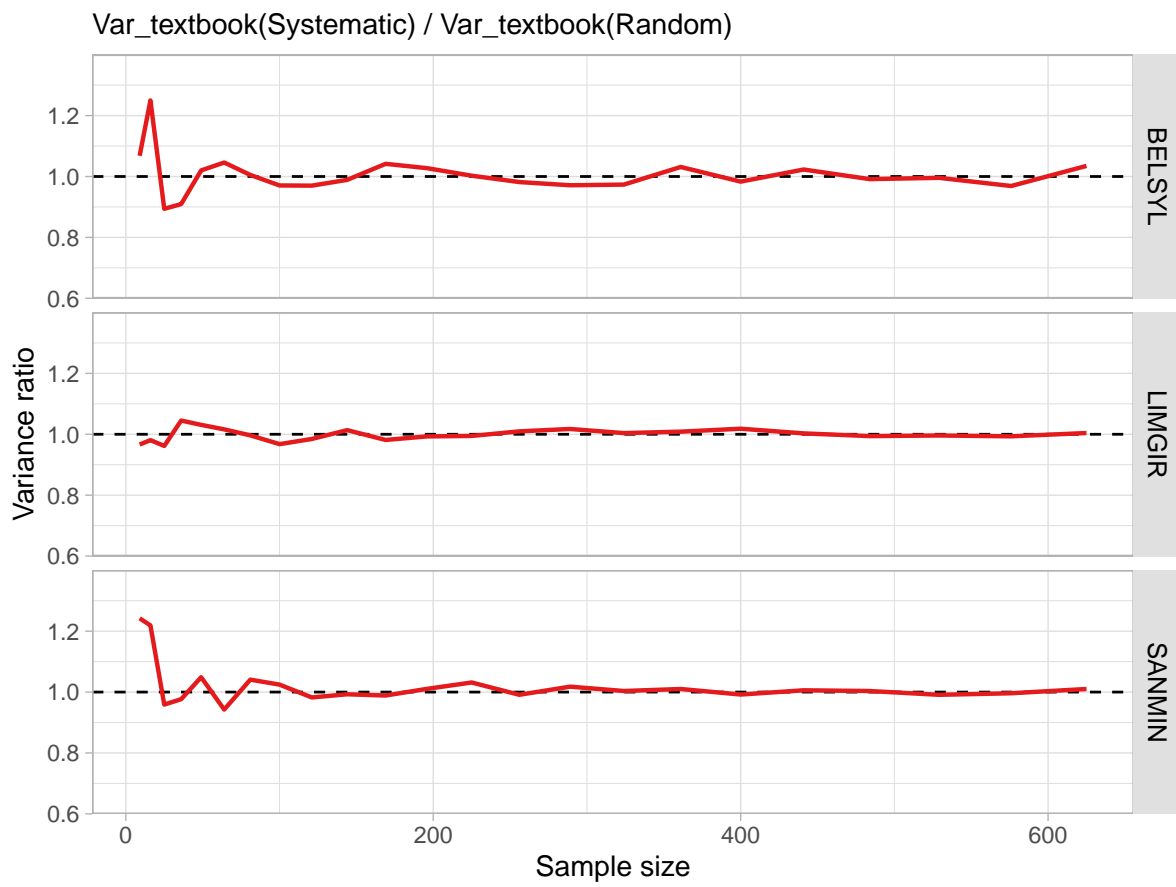


Figure S4.15: Coverage ratio of three variance estimators (V_{textbook} , V_{nbh} and V_{ZIP}) for spatially balanced sampling (SYS), as a function of sample size for the three natural populations.

Interpretation: For small sample sizes (i.e. below $n = 75$), all estimators have poor coverage for the three sampling methods. For sample sizes above $n = 75$, all estimators have a coverage ratio around 0.95, except for V_8 and V_w for SYS, which is due to their tendency to underestimation.

2.3 Comparison of the estimated variance for SYS and SBS to the estimated variance for SRS



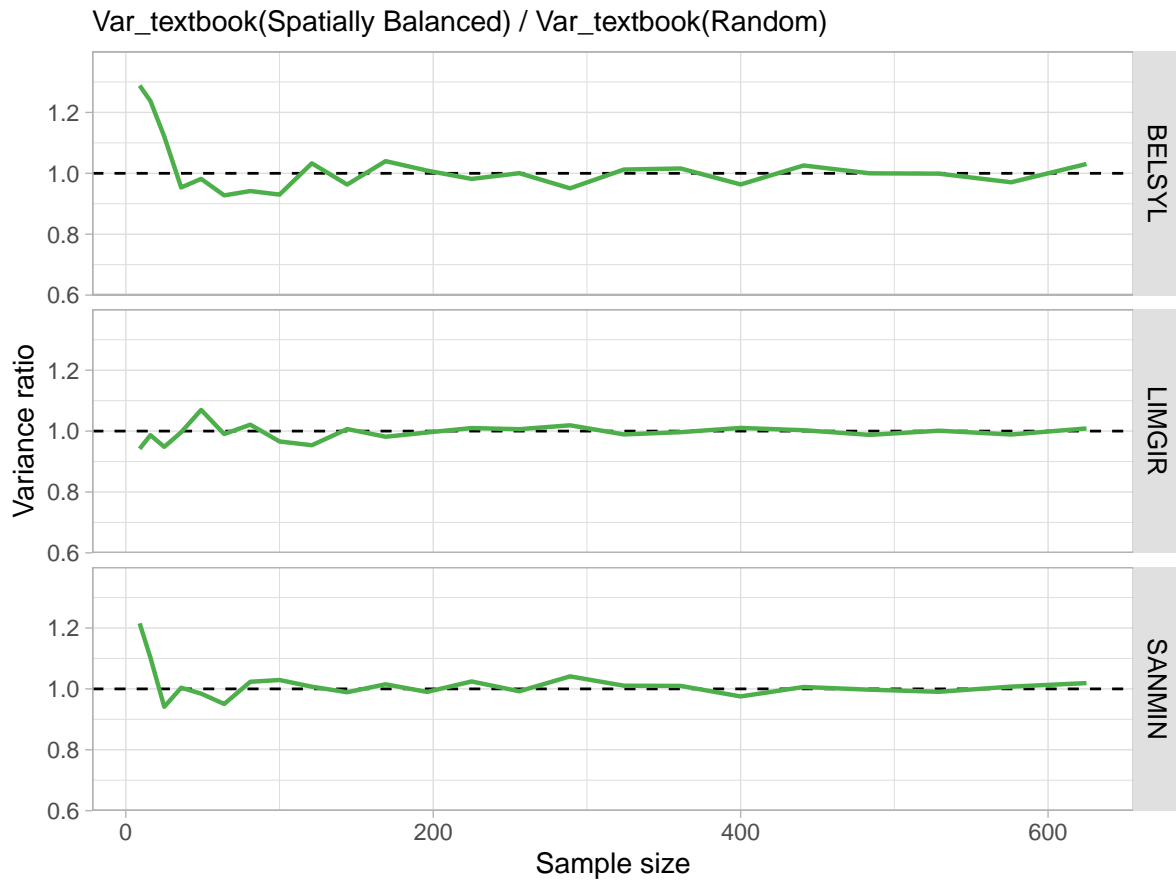
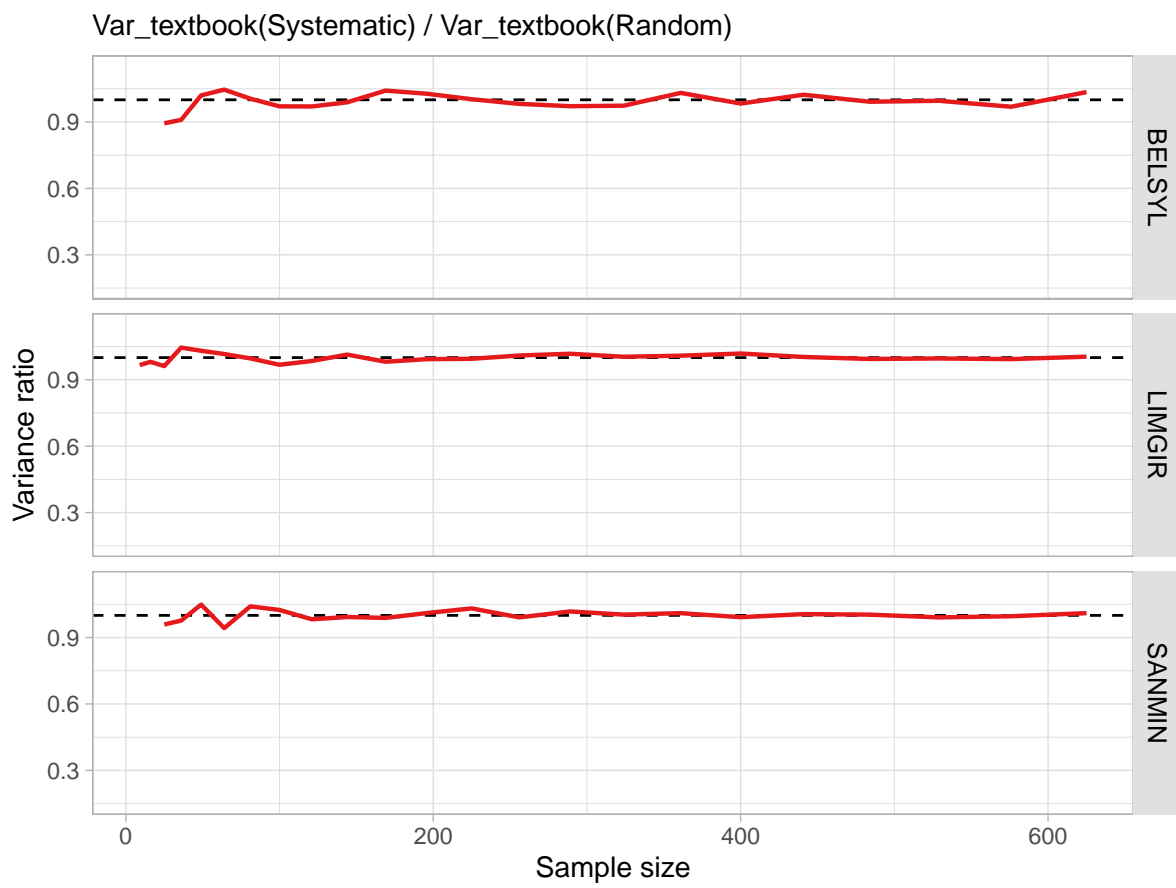
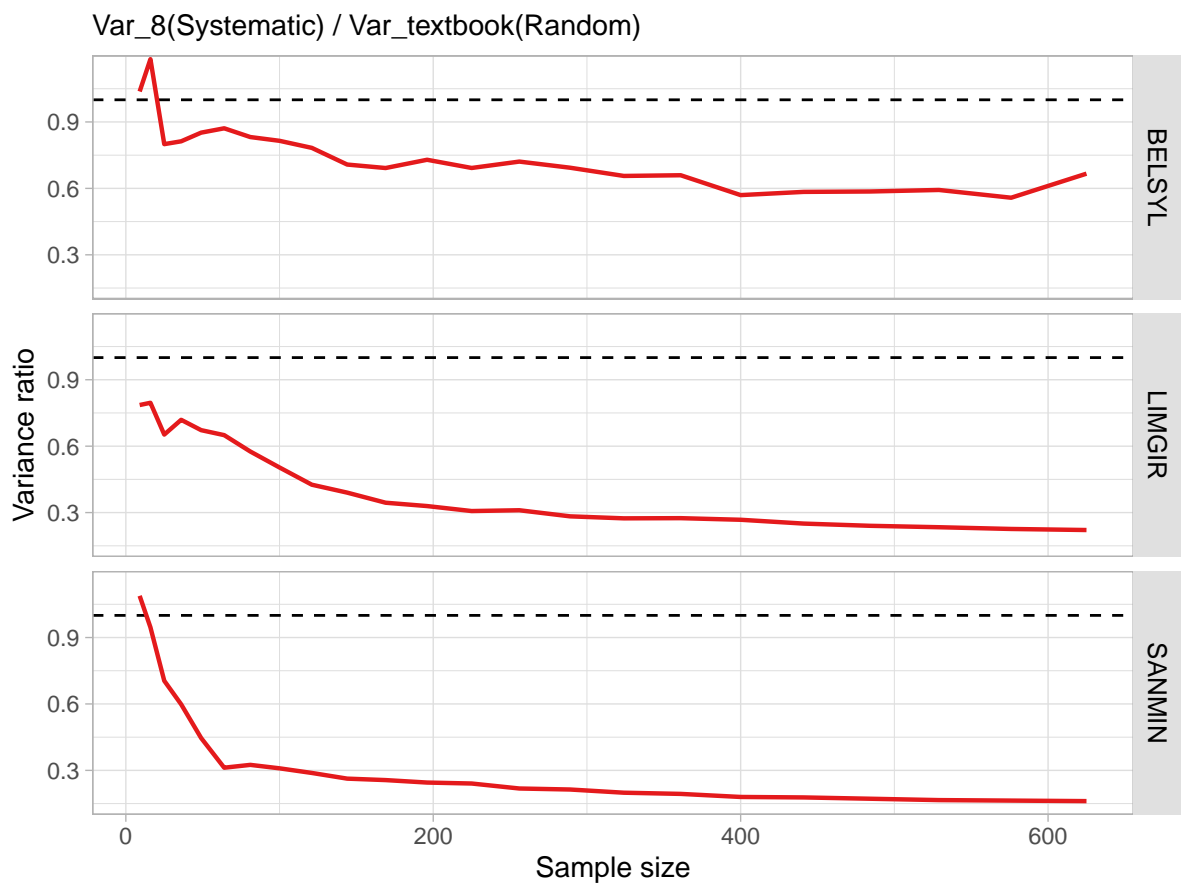
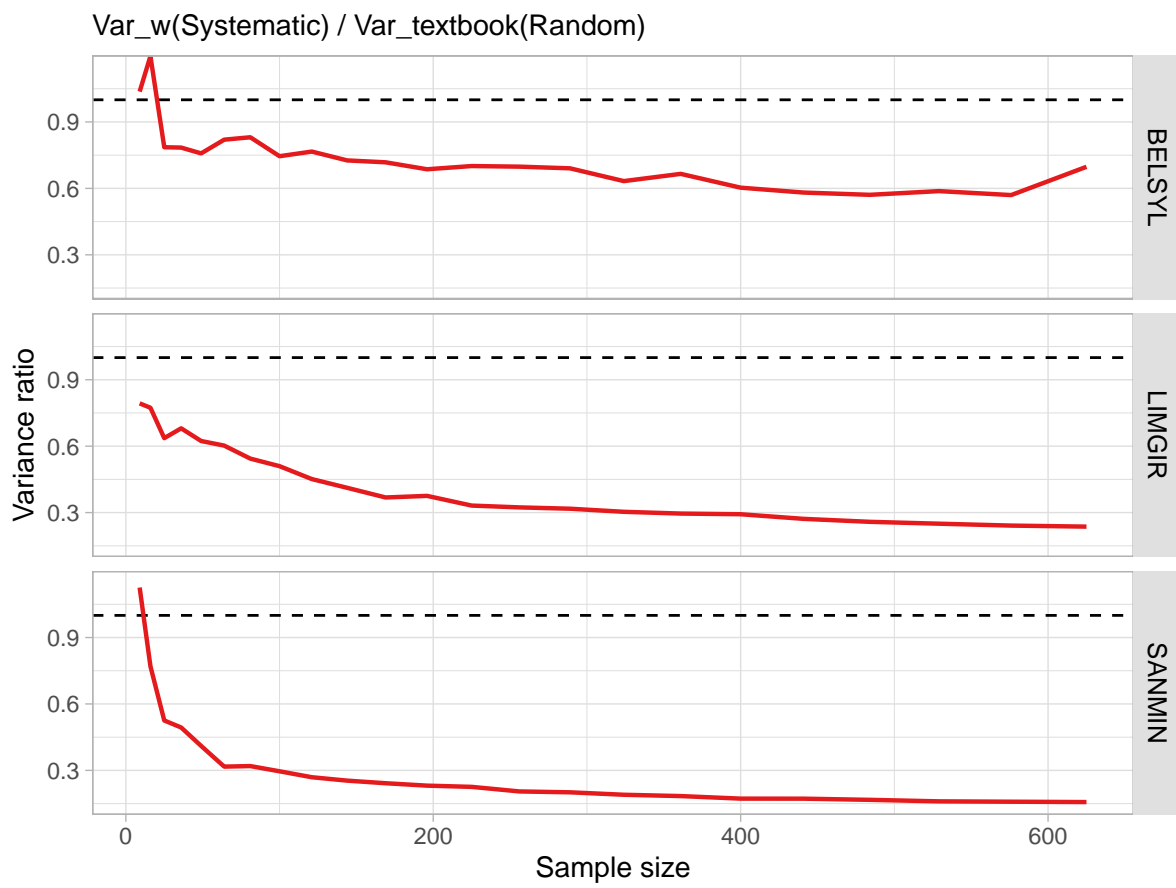
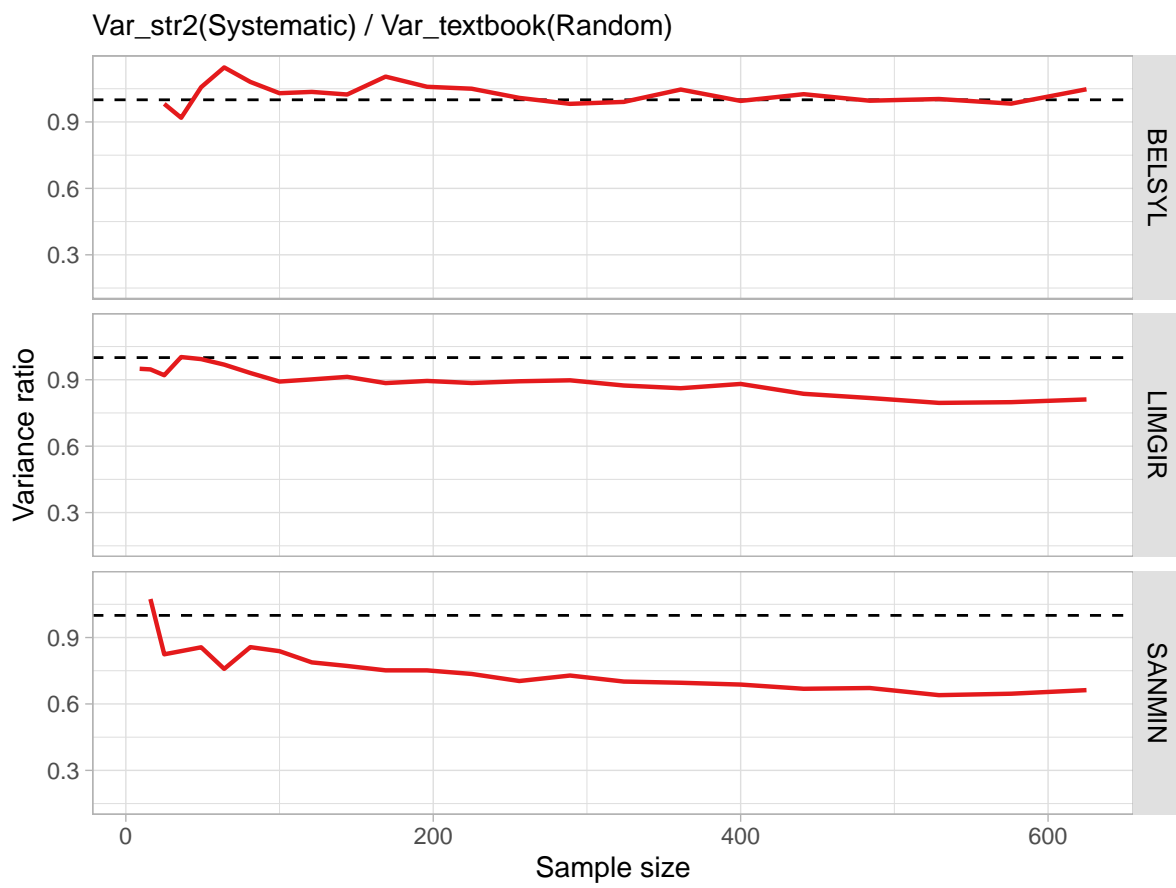


Figure S4.16: Ratio of the variance estimated using the “textbook” estimator for systematic sampling (SYS) and spatially balanced sampling (SBS) over the variance estimated for simple random sampling (SRS), as a function of sample size for the three natural populations.









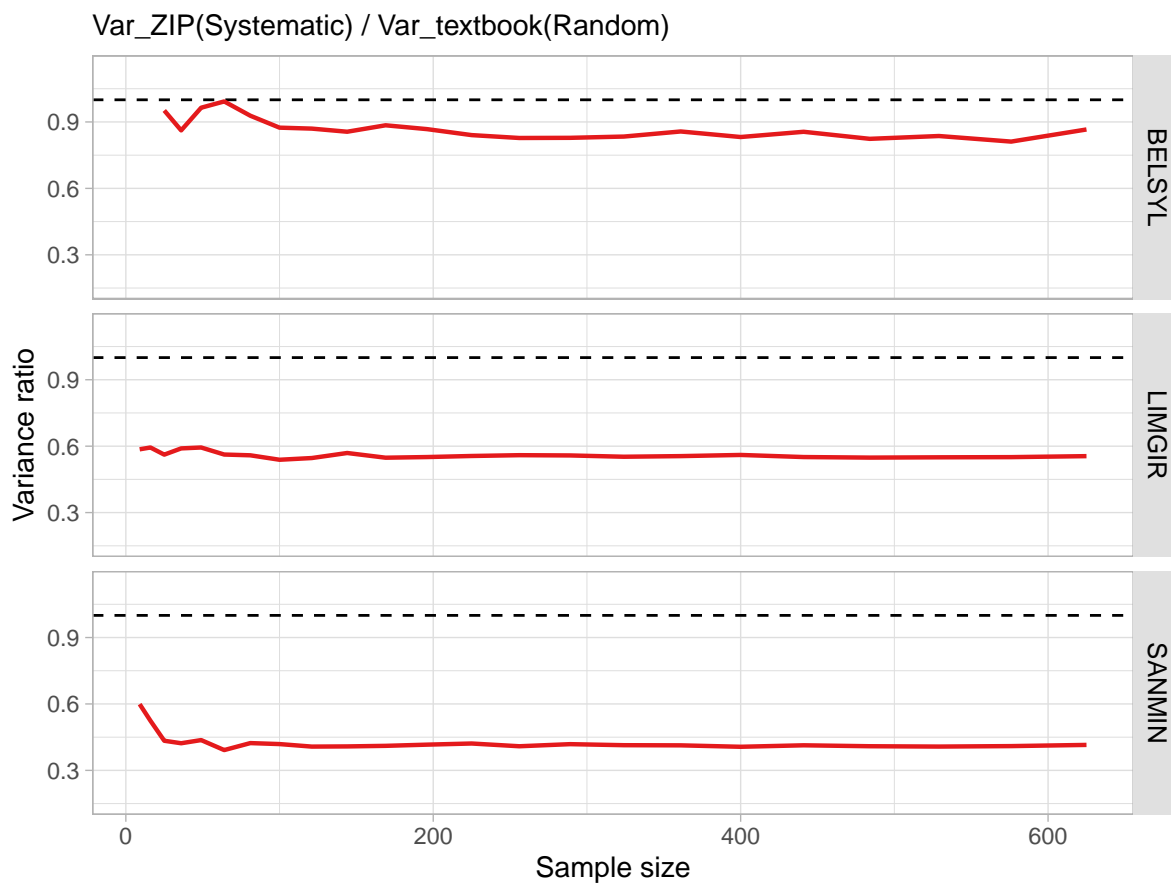
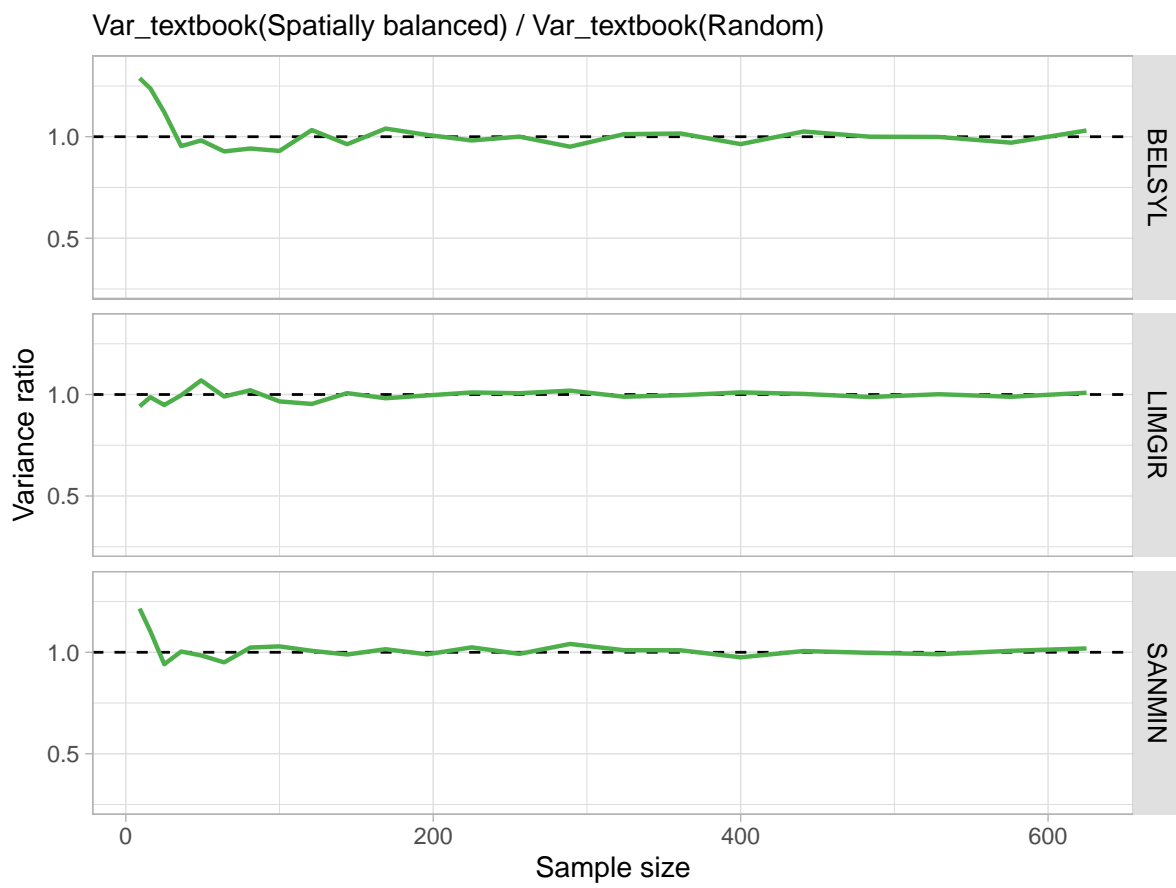
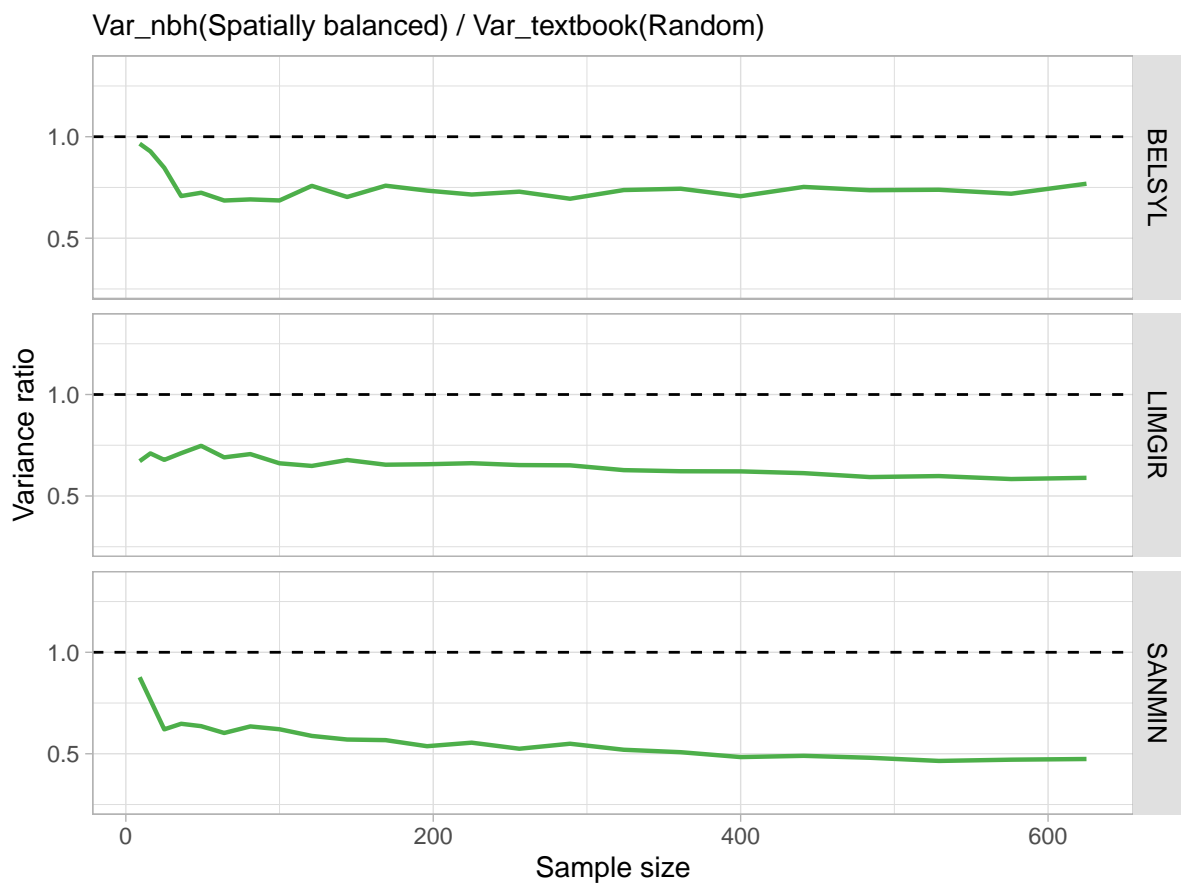


Figure S4.17: Ratio of the variance estimated using five variance estimators (V_{textbook} , V_8 , V_w , V_{str2} , V_{ZIP}) for systematic sampling (SYS) over the variance estimated using the “textbook” estimator for simple random sampling (SRS), as a function of sample size for the three natural populations.





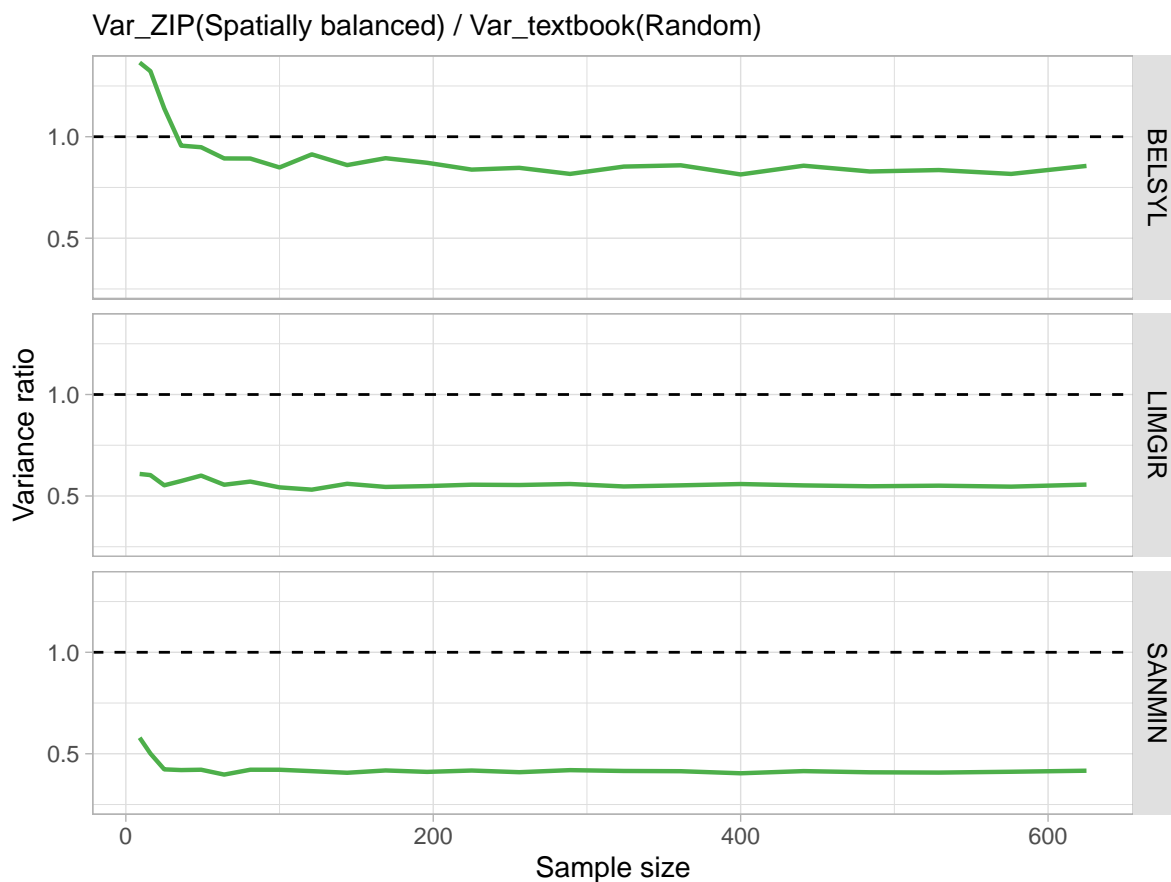


Figure S4.18: Ratio of the variance estimated using three variance estimators (V_{textbook} , V_{nbh} and V_{ZIP}) for spatially balanced sampling (SYS) over the variance estimated using the “textbook” estimator for simple random sampling (SRS), as a function of sample size for the three natural populations.

Interpretation: We have to exclude sample sizes below $n = 75$ from the interpretation because all estimators have a low coverage ratio. We also excluded the estimators V_8 and V_w for SYS, as they underestimate variance for all sample sizes and have an overall low coverage ratio. Using SYS with V_{str2} or V_{ZIP} , or SBS with V_{nbh} or V_{ZIP} , allows for a substantial gain in apparent precision compared to using SRS with V_{textbook} . The gain in apparent precision will be close to the gain in true precision, as these estimators are nearly unbiased.

References

- Beckett, S., Jee, J., Ncube, T., Pompilus, S., Washington, Q., Singh, A., & Pal, N. (2014). Zero-inflated Poisson (ZIP) distribution: Parameter estimation and applications to model data from natural calamities. *Involve, a Journal of Mathematics*, 7(6), 751–767. <https://doi.org/10.2140/involve.2014.7.751>
- Cochran, W. G. (1977). *Sampling Techniques* (3rd ed.). John Wiley & Sons.
- D’Orazio, M. (2003). Estimating the variance of the sample mean in two-dimensional systematic sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, 8(3), 280. <https://doi.org/10.1198/1085711032174>
- Grafström, A., Lundström, N. L. P., & Schelin, L. (2012). Spatially Balanced Sampling through the Pivotal Method. *Biometrics*, 68(2), 514–520. <https://doi.org/10.1111/j.1541-0420.2011.01699.x>
- Jackman, S., Tahk, with contributions from A., Zeileis, A., Maimone, C., & Meers, J. F. and Z. (2020). *pscl*:

- Political Science Computational Laboratory (1.5.5). <https://CRAN.R-project.org/package=pscl>
- Magnussen, S., & Fehrmann, L. (2019). In search of a variance estimator for systematic sampling. *Scandinavian Journal of Forest Research*, 34(4), 300–312. <https://doi.org/10.1080/02827581.2019.1599063>
- Magnussen, S., McRoberts, R. E., Breidenbach, J., Nord-Larsen, T., Ståhl, G., Fehrmann, L., & Schnell, S. (2020). Comparison of estimators of variance for forest inventories with systematic sampling—Results from artificial populations. *Forest Ecosystems*, 7(1), 17. <https://doi.org/10.1186/s40663-020-00223-6>
- McGarvey, R., Burch, P., & Matthews, J. M. (2016). Precision of systematic and random sampling in clustered populations: Habitat patches and aggregating organisms. *Ecological Applications*, 26(1), 233–248. <https://doi.org/10.1890/14-1973>
- Robertson, B. L., Brown, J. A., McDonald, T., & Jaksons, P. (2013). BAS: Balanced Acceptance Sampling of Natural Resources. *Biometrics*, 69(3), 776–784. <https://doi.org/10.1111/biom.12059>
- Stevens, D. L., & Olsen, A. R. (2003). Variance estimation for spatially balanced samples of environmental resources. *Environmetrics*, 14(6), 593–610. <https://doi.org/10.1002/env.606>
- Thompson, S. K. (2012). *Sampling* (3rd ed.). Wiley.
- Wolter, K. M. (2007). *Introduction to Variance Estimation* (2nd ed.). Springer Science & Business Media.

C | Matériel supplémentaire du Chapitre 3

Supplementary Material for “Plants stand still but hide: imperfect and heterogeneous detection is the rule when counting plants”

Jan Perret, Aurélien Besnard, Anne Charpentier, Guillaume Papuga

Created on the 2022-12-21

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Appendix 1: Summary of the field sessions

Table S1.1: Summary of the field sessions.

Species	Date	Locality	Predominant phenological stage	Habitat	Site number	Number of participants
<i>Plantago lanceolata</i>	07/10/2020	Montpellier (34090)	Vegetative	Urban wasteland	1	6
<i>Allium</i> sp.	16/10/2020	Montpellier (34090)	Vegetative	Grassland	2	3
<i>Calendula arvensis</i>	20/10/2020	Montpellier (34090)	Flowering	Grassland	2	5
<i>Sanguisorba minor</i>	28/10/2020	Montpellier (34090)	Vegetative	Urban wasteland	1	5
<i>Allium chamaemoly</i>	05/02/2021	Lattes (34970)	Vegetative	Western Mediterranean scrubland	3	6
<i>Euphorbia helioscopia</i>	04/03/2021	Saint-Jean-de-Vedas (34430)	Flowering	Dry calcareous grassland	4	4
<i>Erodium cicutarium</i>	18/03/2021	Clapiers (34077)	Flowering	Western Mediterranean scrubland	5	6
<i>Chrysosplenium alternifolium</i>	13/04/2021	Valjouffrey (38740)	Flowering	Alpine riparian forest	6	5
<i>Fagus sylvatica</i>	14/04/2021	Gap (05000)	Seedling	Beech forest	7	6
<i>Hieracium</i> sp.	15/04/2021	Le Muy (83490)	Vegetative	Western Mediterranean scrubland	8	7
<i>Bromus rubens</i>	16/04/2021	Marseille (13000)	Flowering	Mediterranean grassland	9	6
<i>Sherardia arvensis</i>	23/04/2021	Clapiers (34077)	Flowering	Western Mediterranean scrubland	5	6
<i>Mentha suaveolens</i>	05/05/2021	Montferrier-sur-Lez (34980)	Vegetative	Lowland hay meadow	10	5
<i>Scabiosa atropurpurea</i>	06/05/2021	Clapiers (34077)	Vegetative	Mediterranean pine forest	11	6
<i>Ornithogalum angustifolium</i>	11/05/2021	Mas-de-Londres (34380)	Flowering	Mediterranean extensive pasture	12	5

Species	Date	Locality	Predominant phenological stage	Habitat	Site number	Number of participants
<i>Evax pygmaea</i>	18/05/2021	Arles (13200)	Flowering	Mediterranean sand annual grassland	13	7
<i>Ophrys lutea</i>	19/05/2021	Mas-de-Londres (34380)	Flowering	Mediterranean extensive pasture	12	5
<i>Carex flacca</i>	26/05/2021	Mas-de-Londres (34380)	Vegetative	Mediterranean extensive pasture	12	6
<i>Anacamptis pyramidalis</i>	27/05/2021	Mas-de-Londres (34380)	Flowering	Mediterranean extensive pasture	12	5
<i>Rumex acetosella</i>	07/06/2021	Orsay (91400)	Flowering	Lowland hay meadow	14	5
<i>Equisetum telmateia</i>	11/06/2021	Orsay (91400)	Vegetative	Megaphorb	15	7
<i>Linaria vulgaris</i>	15/06/2021	Haulme (08800)	Vegetative	Lowland hay meadow	16	7
<i>Melampyrum arvense</i>	16/06/2021	Rancennes (08600)	Flowering	Lowland hay meadow	17	8
<i>Veronica chamaedrys</i>	17/06/2021	Haulme (08800)	Flowering	Frequently mown meadow	18	5
<i>Limonium narbonense</i>	25/06/2021	Le Sambuc (13200)	Vegetative	Salt meadow	19	5
<i>Erigeron annuus</i>	28/06/2021	Creys-Mepieu (38510)	Flowering	Lowland hay meadow	20	5
<i>Ambrosia artemisiifolia</i>	07/07/2021	Avignon (84140)	Vegetative	River gravel bank	21	6
<i>Limonium girardianum</i>	28/07/2021	Le Grau-du-Roi (30240)	Vegetative	Salt steppe	22	6
<i>Euphorbia peplis</i>	29/07/2021	Vic-la-Gardirole (34110)	Flowering	Sand beach	23	7
<i>Epipogium aphyllum</i>	06/08/2021	Crots (05200)	Flowering	Pine forest	24	6

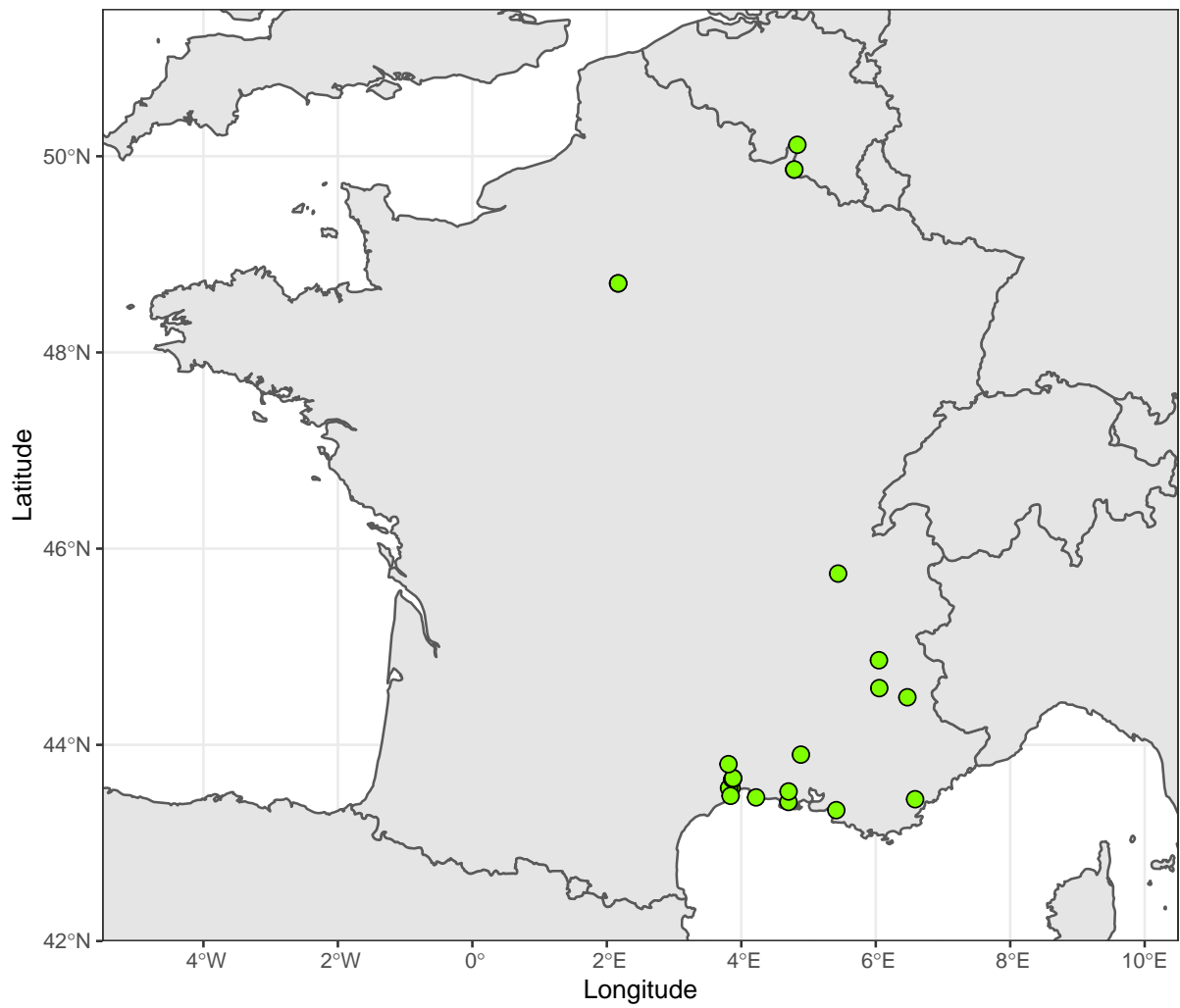


Figure S1.1: Map of the 24 study sites. Some sites were only a few kilometres apart; in this case, the corresponding points overlap.

Appendix 2: Detailed Mat&Meth

Creation of the species conspicuousness variable

For each field session, we visually estimated the mean height range of the individuals of the target species and recorded whether or not the majority of individuals were flowering. Inconspicuous flowers (i.e. without petals or without vivid colours) were not taken into account. We then created the species conspicuousness variable with the following criteria:

- 1 -> Individuals [0 cm; 5 cm] tall, without colourful flowers
- 2 -> Individuals [5 cm; 10 cm] tall, or [0 cm; 5 cm] with colourful flowers
- 3 -> Individuals [10 cm; 20 cm] tall, without colourful flowers
- 4 -> Individuals [20 cm; +Inf[tall, or [10 cm; 20 cm] with colourful flowers

Table S2.1: Value of the species conspicuousness variable for the 30 sampled species (1 = least conspicuous; 4 = most conspicuous).

Species name	Species code	Species conspicuousness	Date
<i>Allium chamaemoly</i>	ALLCHA	1	05/02/2021
<i>Bromus rubens</i>	BRORUB	1	16/04/2021
<i>Carex flacca</i>	CARFLA	1	26/05/2021
<i>Erodium cicutarium</i>	EROCIC	1	18/03/2021
<i>Euphorbia peplis</i>	EUPPEP2	1	29/07/2021
<i>Evax pygmaea</i>	EVAPYG	1	18/05/2021
<i>Fagus sylvatica</i>	FAGSYL	1	14/04/2021
<i>Limonium girardianum</i>	LIMGIR	1	28/07/2021
<i>Plantago lanceolata</i>	PLALAN	1	07/10/2020
<i>Sherardia arvensis</i>	SHEARV	1	23/04/2021
<i>Allium</i> sp	ALLsp	2	16/10/2020
<i>Ambrosia artemisiifolia</i>	AMBART	2	07/07/2021
<i>Calendula arvensis</i>	CALARV2	2	20/10/2020
<i>Chrysosplenium alternifolium</i>	CHRALT	2	13/04/2021
<i>Epipogium aphyllum</i>	EPIAPH	2	06/08/2021
<i>Hieracium</i> sp	HIEsp	2	15/04/2021
<i>Ophrys lutea</i>	OPHLUT	2	19/05/2021
<i>Rumex acetosella</i>	RUMACE	2	07/06/2021
<i>Sanguisorba minor</i>	SANMIN	2	28/10/2020
<i>Scabiosa atropurpurea</i>	SCAATR	2	06/05/2021
<i>Euphorbia helioscopia</i>	EUPHEL	3	04/03/2021
<i>Limonium narbonense</i>	LIMNAR	3	25/06/2021

Species name	Species code	Species conspicuousness	Date
<i>Linaria vulgaris</i>	LINVUL	3	15/06/2021
<i>Melampyrum arvense</i>	MELARV	3	16/06/2021
<i>Ornithogalum angustifolium</i>	ORNANG	3	11/05/2021
<i>Veronica chamaedrys</i>	VERCHA	3	17/06/2021
<i>Anacamptis pyramidalis</i>	ANAPYR	4	27/05/2021
<i>Equisetum telmateia</i>	EQUTEL	4	11/06/2021
<i>Erigeron annuus</i>	ERIANN	4	28/06/2021
<i>Mentha suaveolens</i>	MENSUA	4	05/05/2021

Creation of the habitat closure variable

For each quadrat, we visually estimated the proportion of the area covered by vegetation, using the cells as a guide. We also measured the height of the vegetation at 9 identical points in each quadrat, marked by the intersections of the elastic bands forming the cells (Fig. S2.1). The median of these 9 measurements was used as a measure of the height of the vegetation in each quadrat.

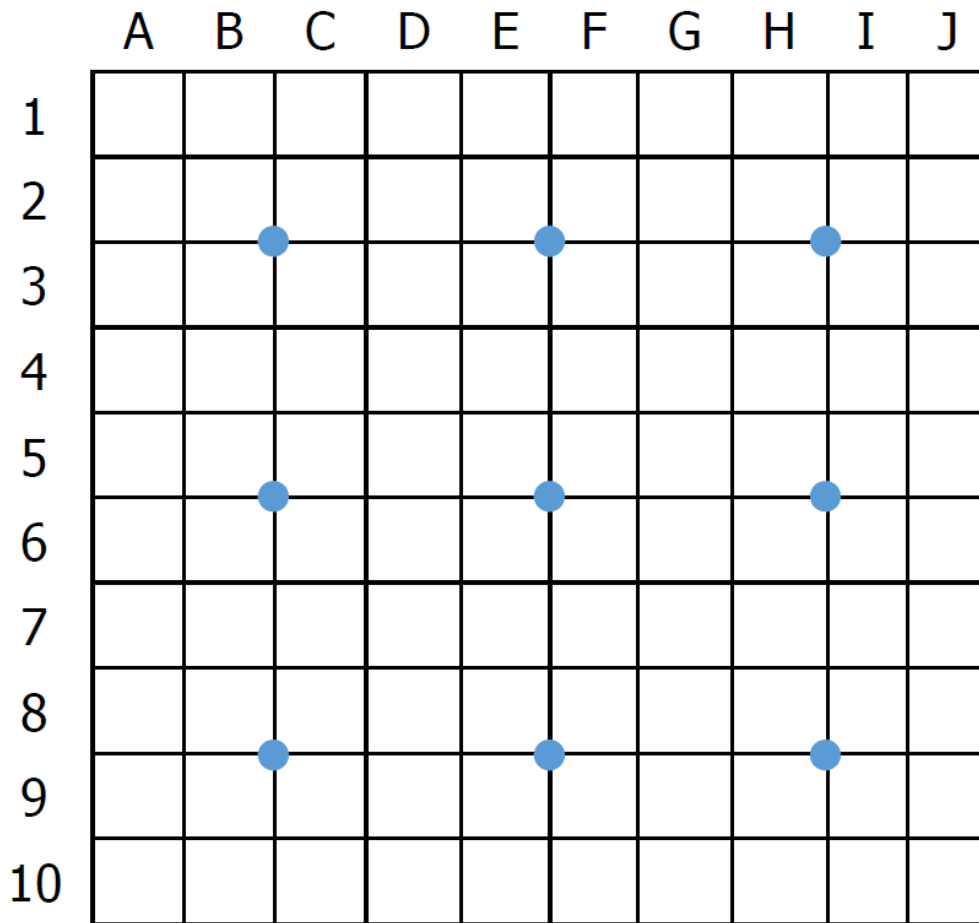


Figure S2.1: Diagram with the location of the points (in blue) where we measured vegetation height in each quadrat.

In order to obtain a synthetic measure of vegetation closure, we performed a PCA on the two variables (i.e. vegetation cover proportion and vegetation height) and kept the quadrat coordinates on the first principal component.

The first principal component explained 77.18% of the total variance, and the second explained 22.82% of the variance. Figure S2.2 shows the value associated with each quadrat on the first principal component, i.e. our new composite variable of habitat closure, as a function of the cover and height of the vegetation.

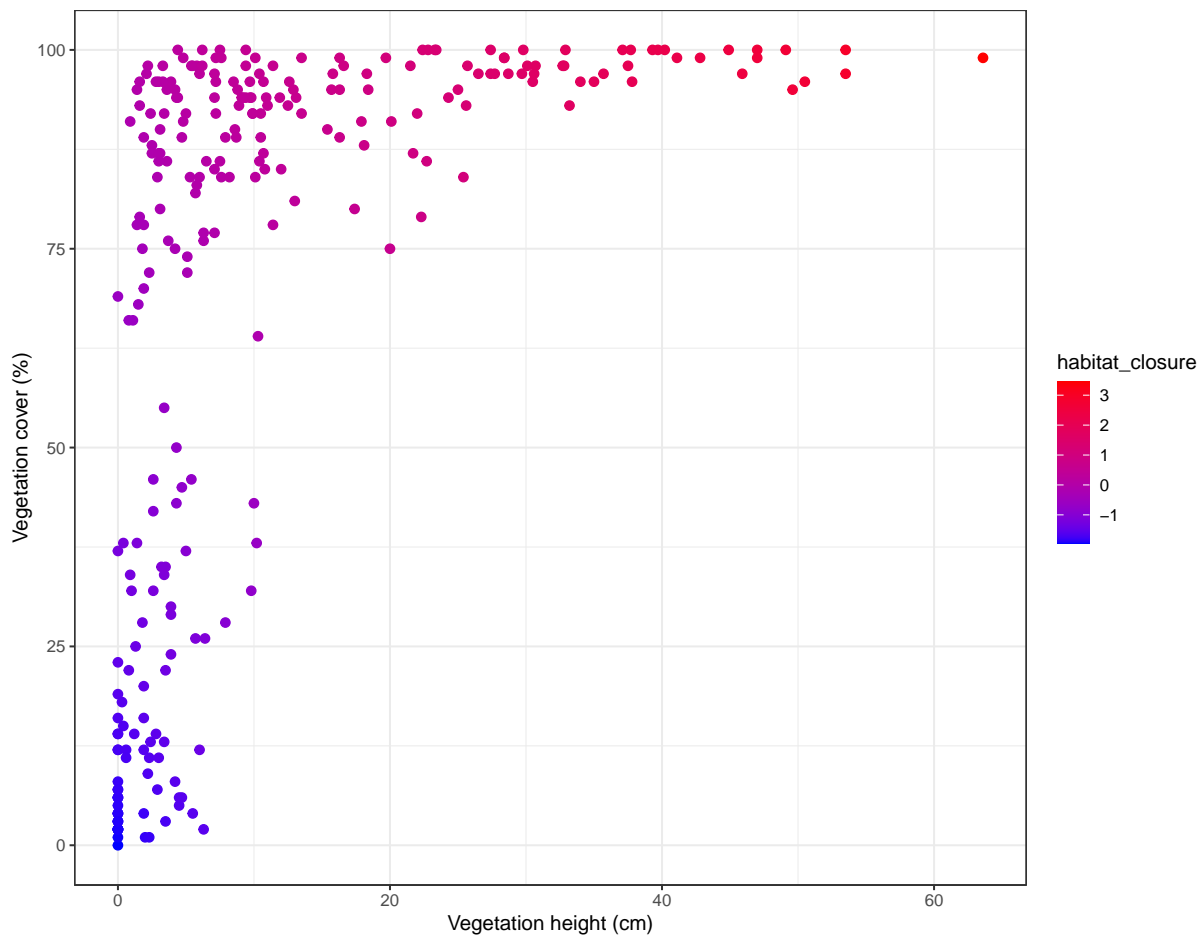


Figure S2.2: Value of the ‘habitat closure’ variable as a function of vegetation height and cover (-1 = least closed; 3 = most closed).

Evaluation of the experience in botany of the observers

Before we explained the experiment to the observers, they were asked to fill in a form including a rating of their level of experience in botany on a scale of 1 to 10. In order to standardise the ratings between observers of all field sessions, a brief description was provided for every second level of this experience scale. We subsequently divided the experience level by two to obtain a scale with 5 classes (1 = least experienced; 5 = most experienced).

The form was as follows:

How do you evaluate your experience in botany? (circle your level) The number of known species is given as a guide. If the description of a level fits, but you can easily recognise more species than the indicated range, you can choose the higher category if you feel that it better fits your experience level. A ‘known species’ means that you can identify it with certainty without using an identification guide, or simply by quickly checking a single criterion.

1

2: You have previously practised botany but rarely do so now or have not practised at all for a long time. (Less than 50 known species)

3

4: You practice botany occasionally, or you started less than 3 years ago. (50–300 known species)

5

6: You practice botany regularly and have done so for more than 3 years. (300–1000 known species)

7

8: You have been practising botany intensively for more than 5 years and are developing expertise. (1000–2000 known species)

9

10: You have been practising botany intensively for more than 10 years and are recognised as an expert. (More than 2000 known species)

Appendix 3: Data visualisation

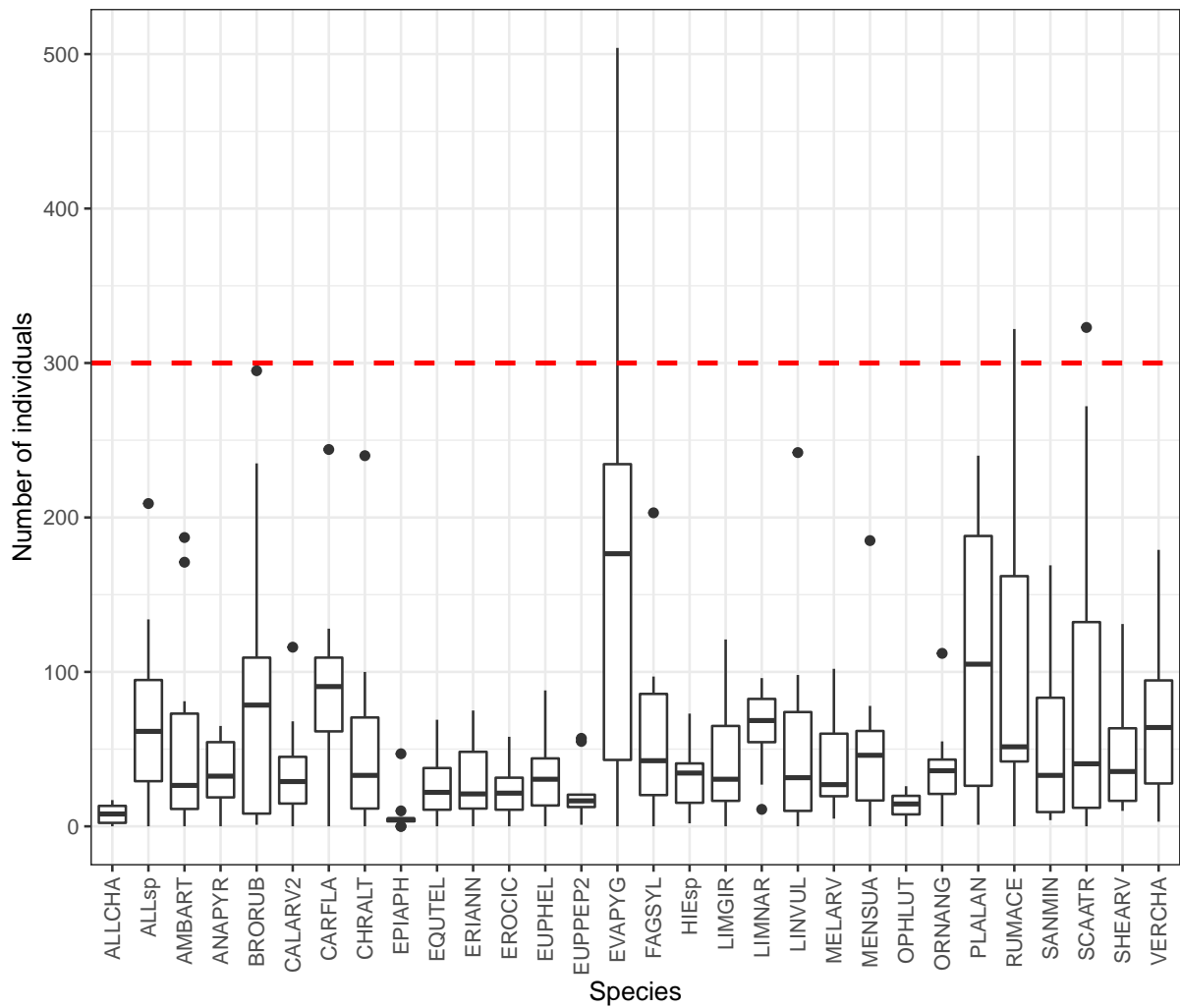


Figure S3.1: The true number of individuals per quadrat and field session, before the four density outliers were removed. The dotted red line shows the threshold of 300 individuals above which we removed the quadrats from the dataset to avoid the leverage effect.

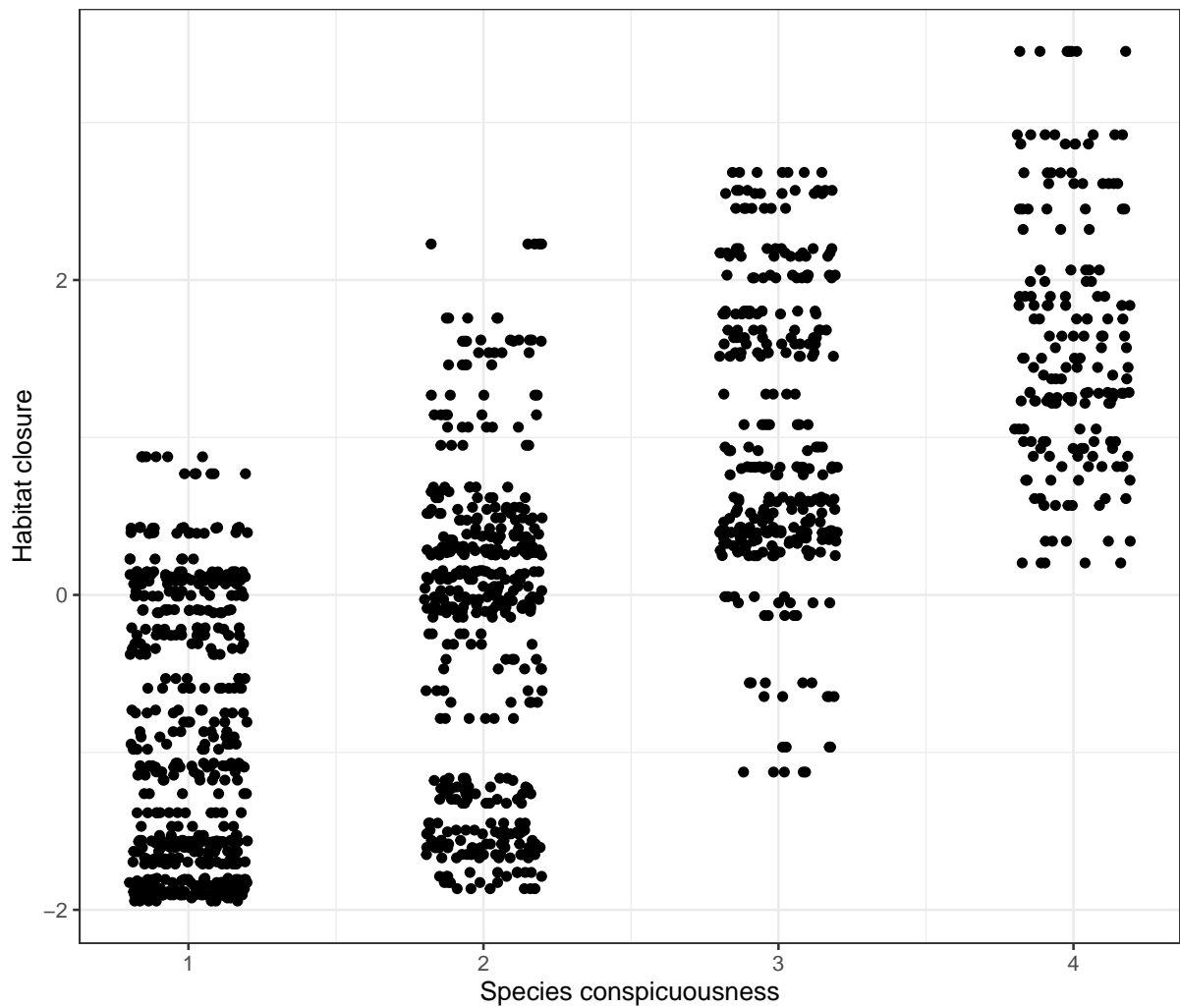
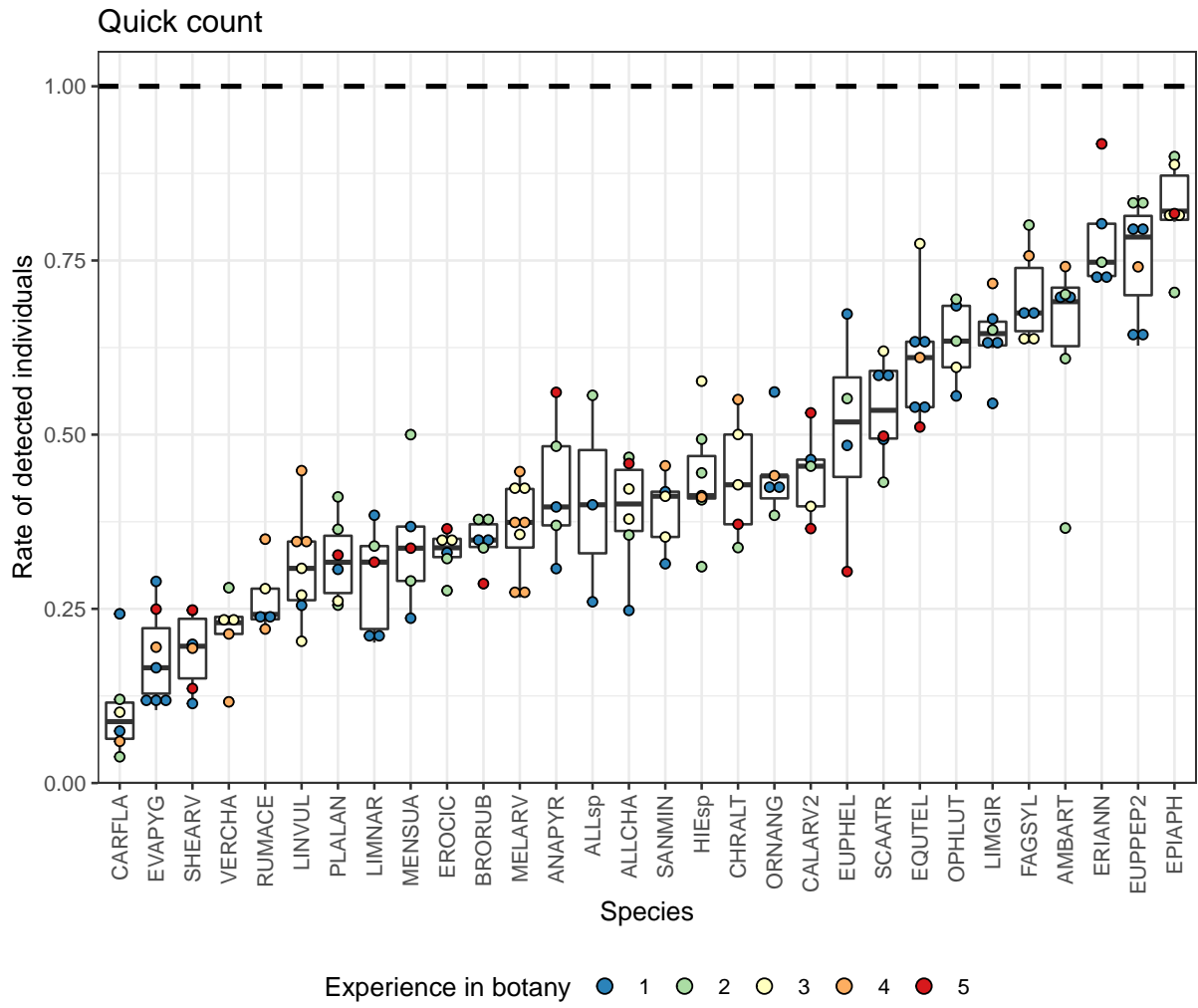
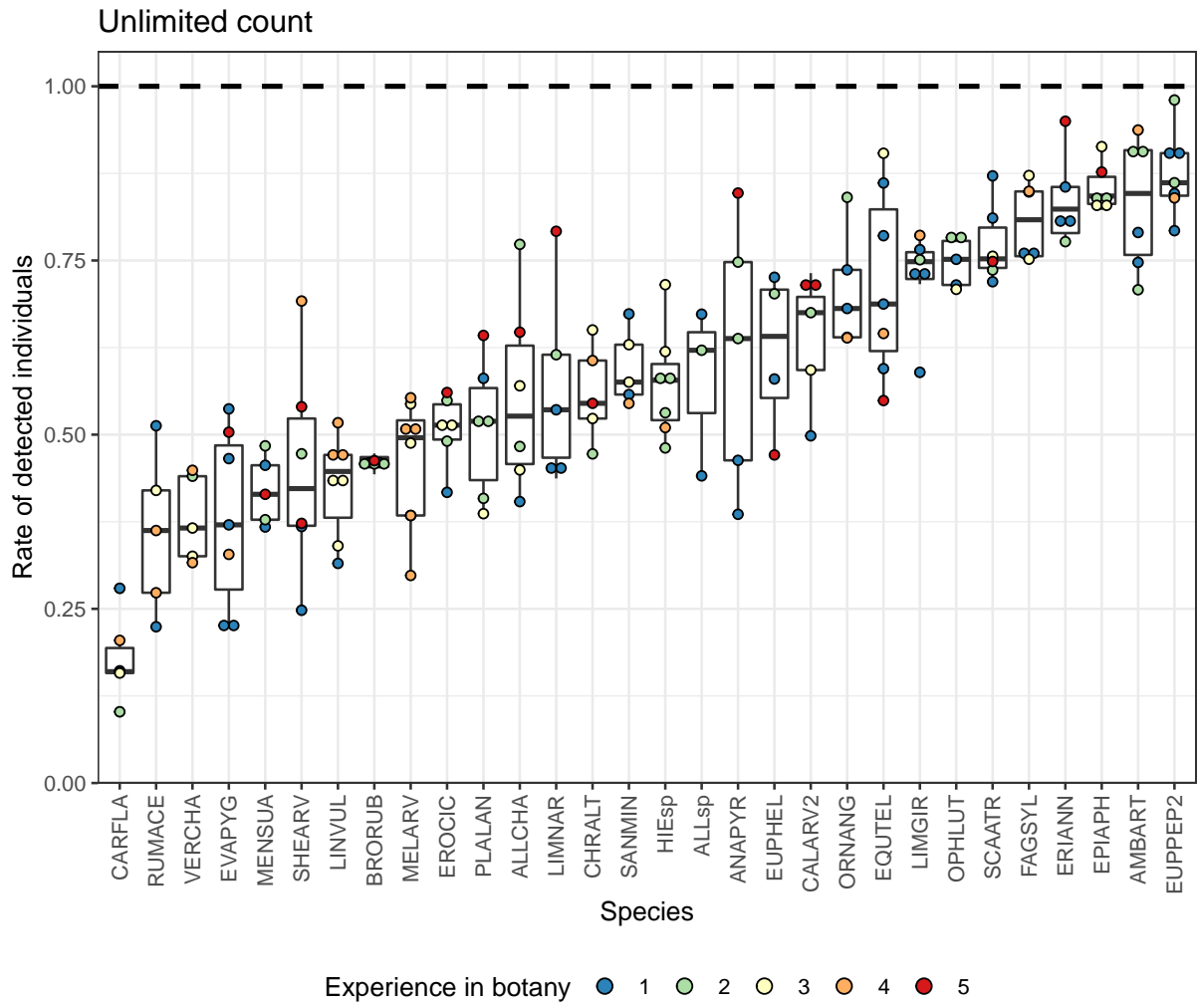


Figure S3.2: Distribution of the observations depending on the conspicuousness of the studied species and the habitat closure. Each point represents an observation by a participant on a quadrat for the first counting method, i.e. only one-third of the observations are represented. Random noise was added to the position of the points on the x-axis so that they do not overlap. The combinations that do not exist in the dataset, i.e. a very inconspicuous species in a very closed habitat or a very conspicuous species in a very open habitat, are uncommon in the field.





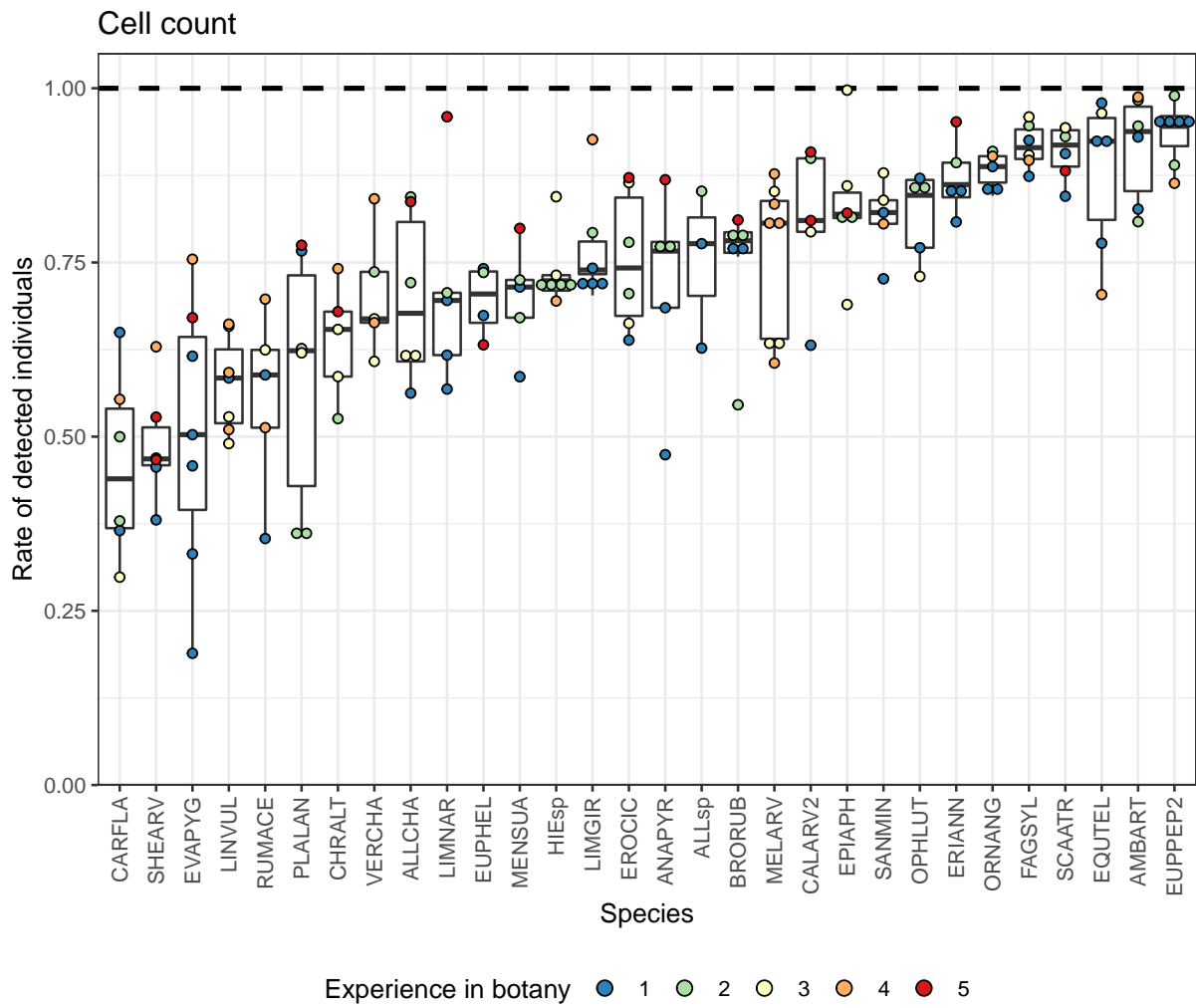


Figure S3.3: Mean proportion of detected individuals per observer after the excess detections were removed. Each point represents the mean detection proportion of an observer during a field session, with 1.00 being perfect detection. The colours indicate the observer’s experience in botany (1 = least experienced; 5 = most experienced).

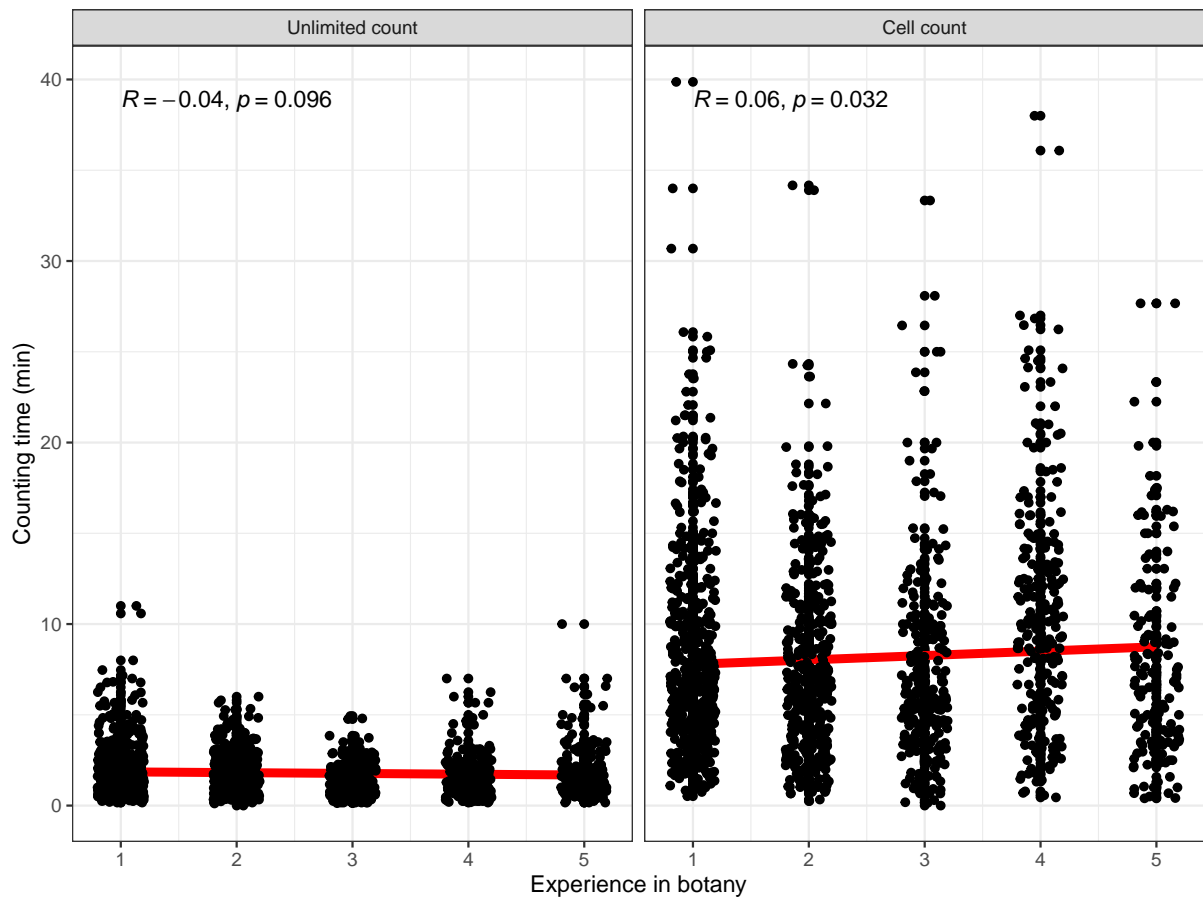


Figure S3.4: Distribution of the counting times depending on the level of experience in botany of the observers. Random noise was added to the position of the points on the x-axis so that they do not overlap. The red lines show basic linear regressions, and the values written in the top left corner are Pearson's correlation coefficients and the p-value of the associated test.

Appendix 4: Description of the excess detections

The dataset was composed of a total of 5024 observations before removing the 34 quadrats that did not contain any individual of the target species. 565 observations were made in these empty quadrats, only 12 of which with excess detections. This seems to indicate that identification errors were extremely rare during the experiment, and that the excess detections were mainly due to errors in differentiating individuals.

The description below refers to the dataset after removing the quadrats that did not contain any individual of the target species. After this filtering, the dataset contained 4459 observations, of which 140 excess detections.

Table S4.1: Distribution of the observations with excess detections per field session.

Species	Total number of observations	Number of excess detections	Proportion of excess detections
ALLCHA	144	2.000	0.014
ALLsp	80	0.000	0.000
AMBART	144	6.000	0.042
ANAPYR	120	1.000	0.008
BRORUB	180	6.000	0.033
CALARV2	135	4.000	0.030
CARFLA	143	0.000	0.000
CHRALT	120	7.000	0.058
EPIAPH	144	0.000	0.000
EQUTEL	180	7.000	0.039
ERIANN	120	32.000	0.267
EROCIC	162	1.000	0.006
EUPHEL	108	6.000	0.056
EUPPEP2	210	9.000	0.043
EVAPYG	122	0.000	0.000
FAGSYL	161	11.000	0.068
HIEsp	210	10.000	0.048
LIMGIR	162	6.000	0.037
LIMNAR	146	2.000	0.014
LINVUL	168	1.000	0.006
MELARV	240	1.000	0.004
MENSUA	120	0.000	0.000
OPHLUT	120	7.000	0.058
ORNANG	135	0.000	0.000
PLALAN	180	8.000	0.044
RUMACE	105	0.000	0.000

Species	Total number of observations	Number of excess detections	Proportion of excess detections
SANMIN	150	2.000	0.013
SCAATR	126	8.000	0.063
SHEARV	175	2.000	0.011
VERCHA	149	1.000	0.007

The observations with excess detections made up less than 6.8% of the observations per field session, except for the session on *Erigeron annuus* (ERIANN; 26.7% observations over 100% detection). For this field session the detection of individuals was very easy as the individuals were in full flower and taller than the surrounding vegetation, which resulted in a high detection rate. Furthermore, many individuals had multiple stems and the ramification was close to the ground. It was possible to differentiate the individuals unambiguously by looking closely at the ramification, but the observers did not pay close attention. This combination of easy detection and the particular morphology of individuals led to these excess detections.

Table S4.2: Distribution of the observations with excess detections per level of botany experience (1 = least experienced; 5 = most experienced).

Experience in botany	Total number of observations	Number of excess detections	Proportion of excess detections
1.000	1,474	57.000	0.039
2.000	1,095	28.000	0.026
3.000	790	25.000	0.032
4.000	641	14.000	0.022
5.000	459	16.000	0.035

The excess detections are roughly evenly distributed across the levels of experience in botany.

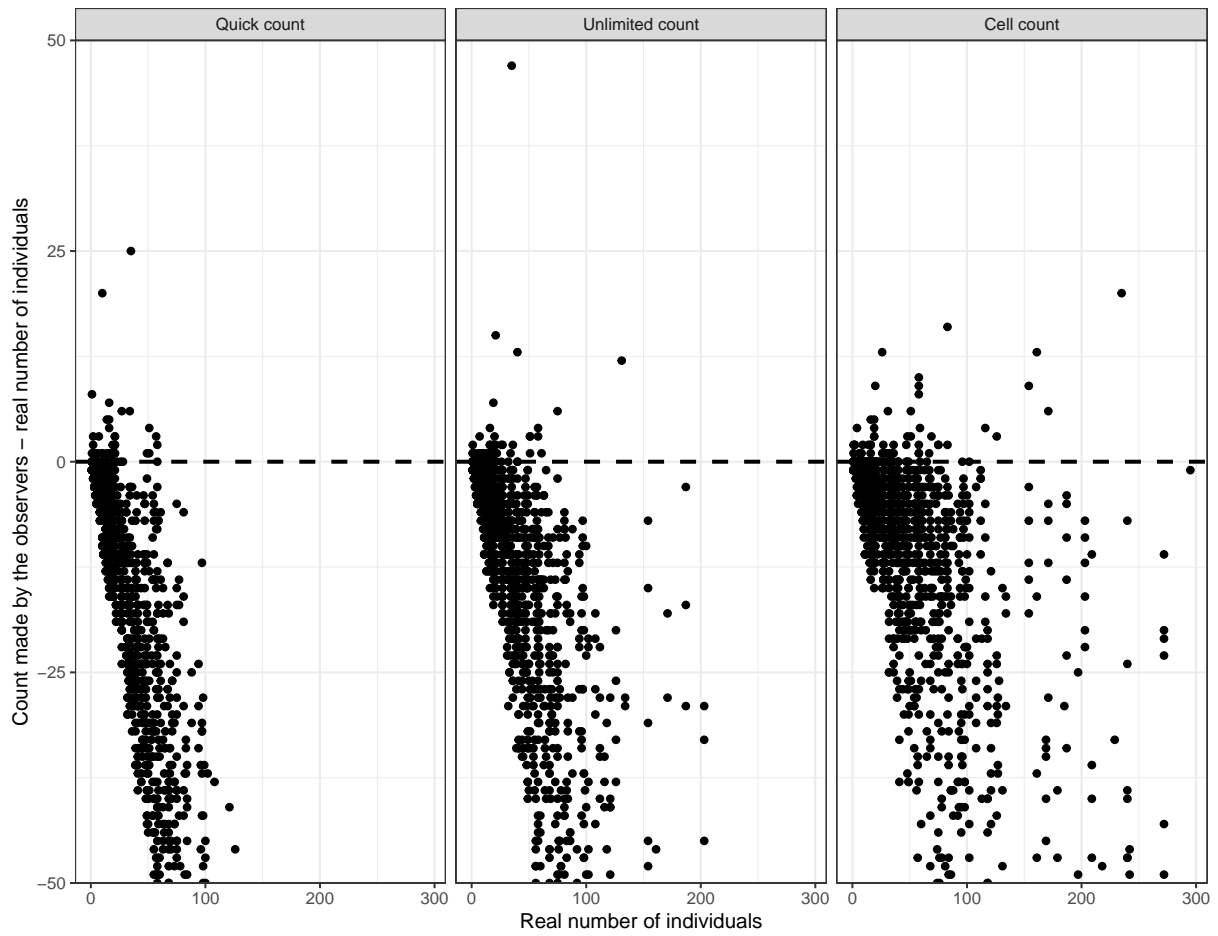
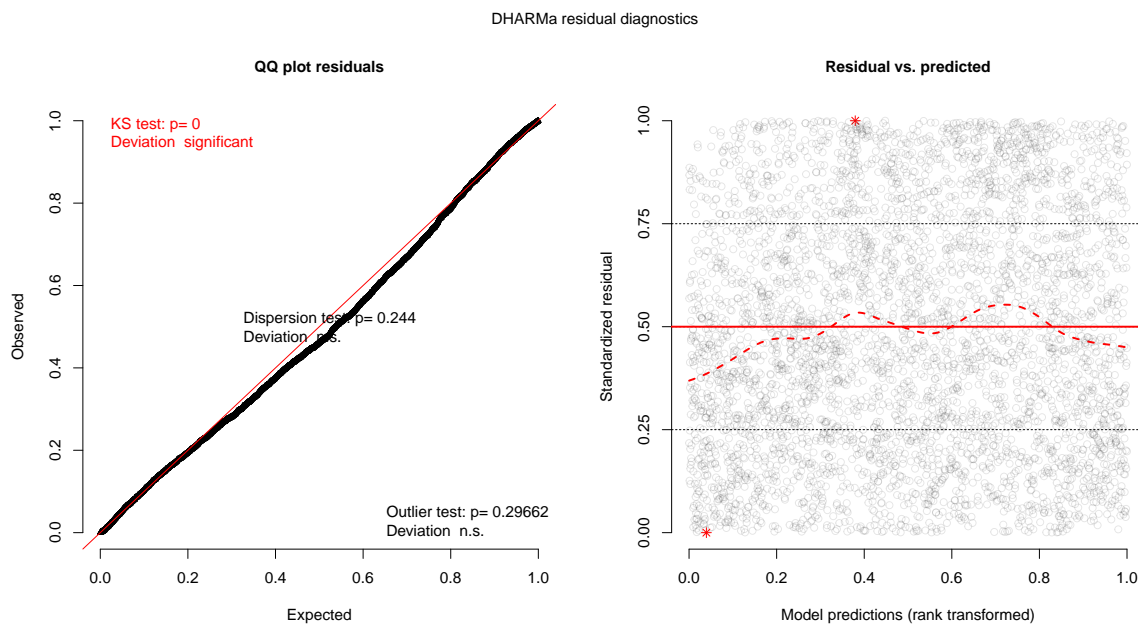


Figure S4.1: Difference between the counts made by the observers and the true number of individuals present in the quadrats. The lower part of the graph is truncated, but not the upper part, so all excess detections are represented. The majority of the excess detections occurred in quadrats containing few individuals, and were below 110% of the true number of individuals.

Appendix 5: Model goodness-of-fit assessment

We assessed the goodness-of-fit of the model using the R package DHARMA (Hartig, 2022). This package uses a simulation approach to produce scaled residuals for Generalised Linear Mixed Models (GLMMs), which can be interpreted as residuals from classic linear models to assess a model's fit. For a detailed explanation of how the package works and how to interpret residual diagnostic plots, see the vignette of the package here: <https://cran.r-project.org/web/packages/DHARMA/vignettes/DHARMA.html>

Main residual diagnostic plots

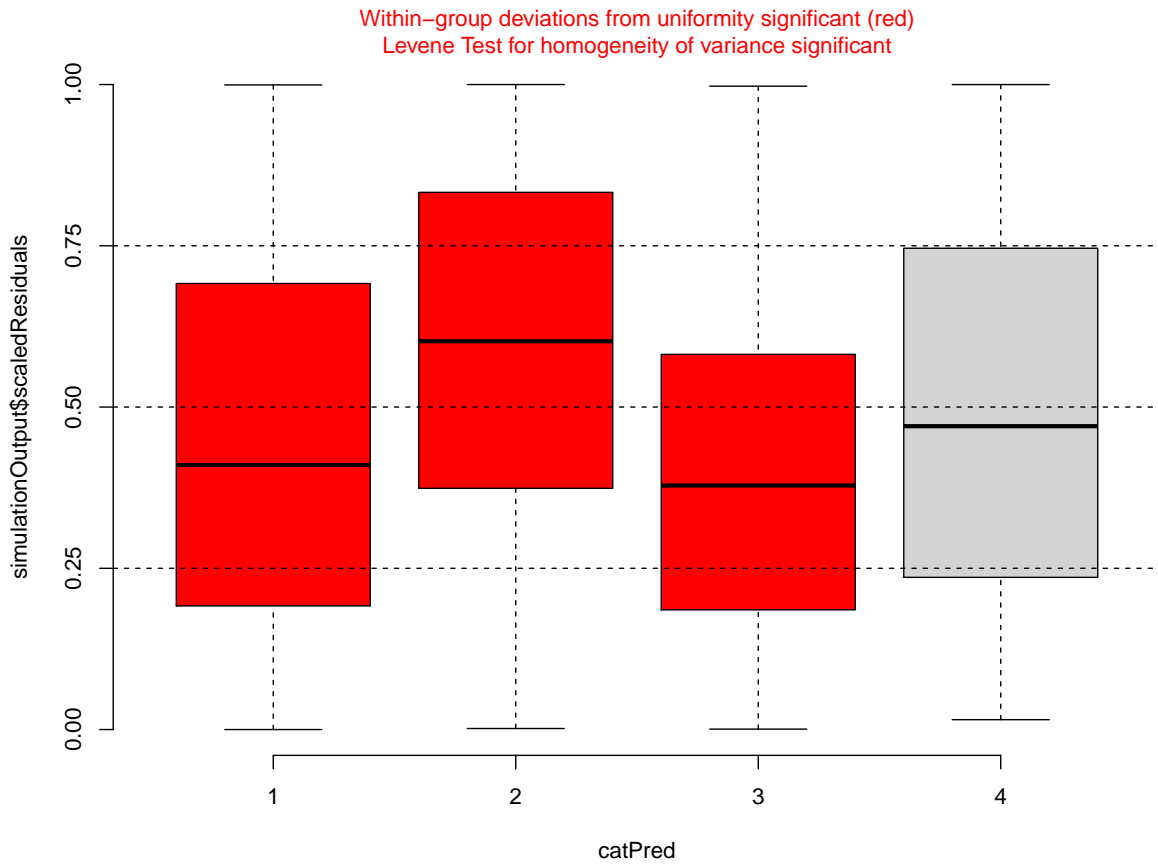


Overall the model fit seems very good ! On the quantile-quantile plot (left) there is a slight deviation from the $x=y$ line, but this deviation is very small. On the three tests performed by the DHARMA package, the dispersion test and the outlier test are non-significant, which means that the simulated dispersion is equal to the observed dispersion and that there are no simulation outliers, respectively. However the KS uniformity test is significant, which seems logical given the deviation we can see on the QQ plot and the large number of observations in the dataset. A visual inspection of the QQ plot shows that although the deviation exists, it is small. It seems unlikely that this could substantially affect the model estimates, especially given the robustness of GLMMs to violations of distributional assumptions (Schielzeth et al., 2020). The residuals against predicted values plot (right) supports this interpretation, as there is no clear pattern in the residuals.

Residuals against predictors plots

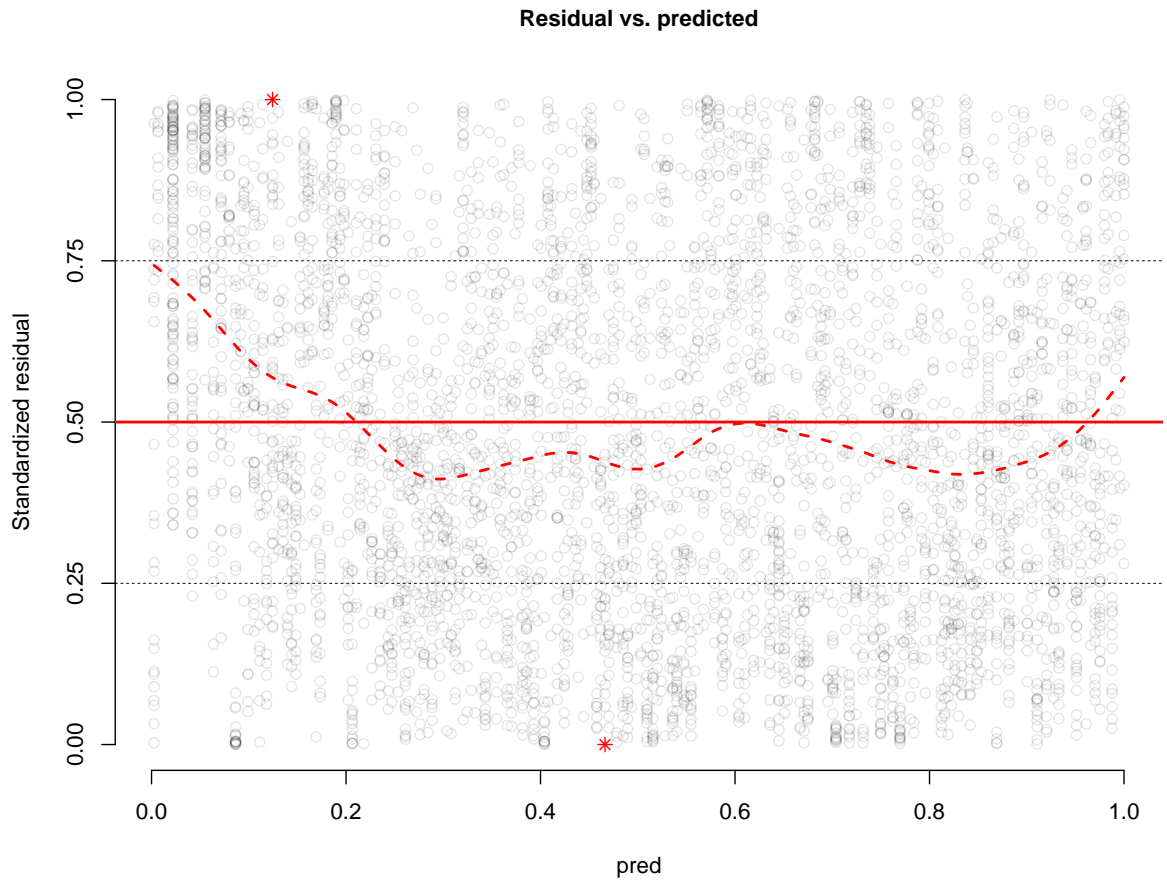
We now plot the residuals against the predictors in the model to check if there is a lack of fit for some predictor.

Species conspicuousness



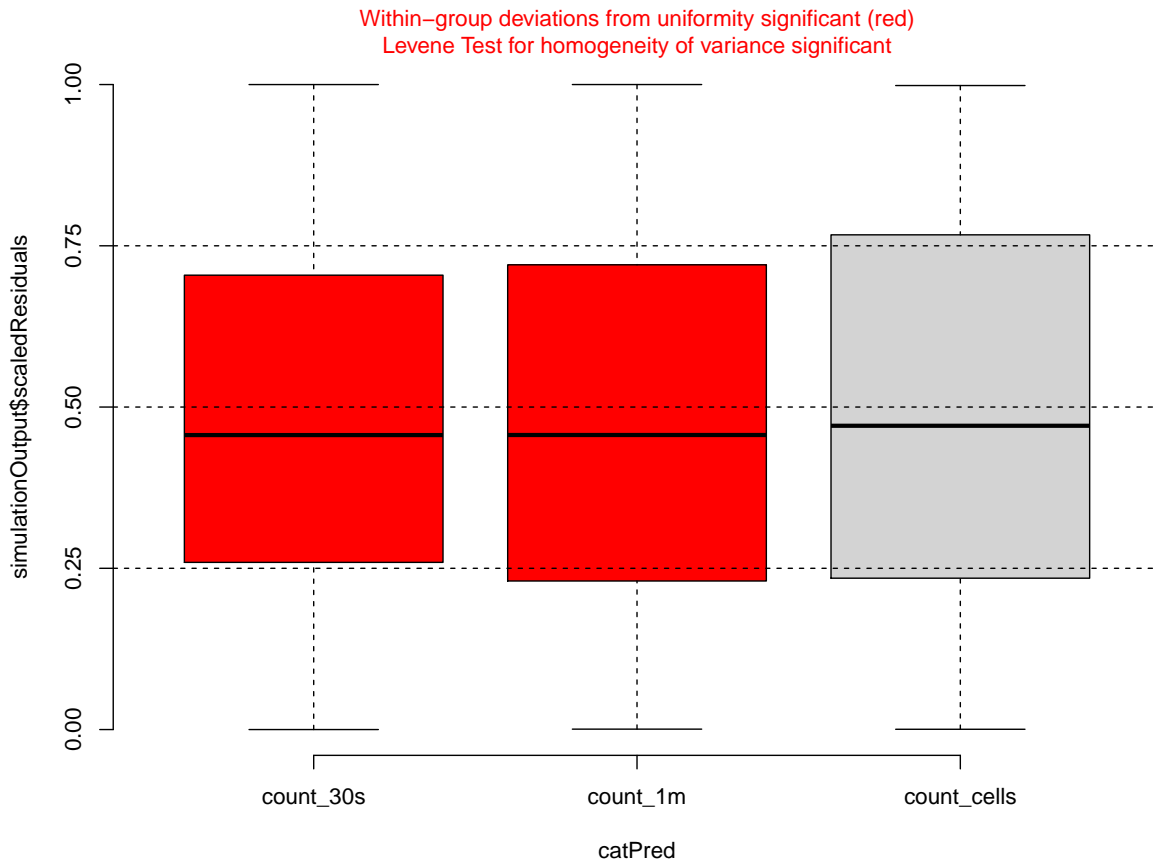
There is a slight deviation from the expected distribution, but no systematic pattern.

Habitat closure



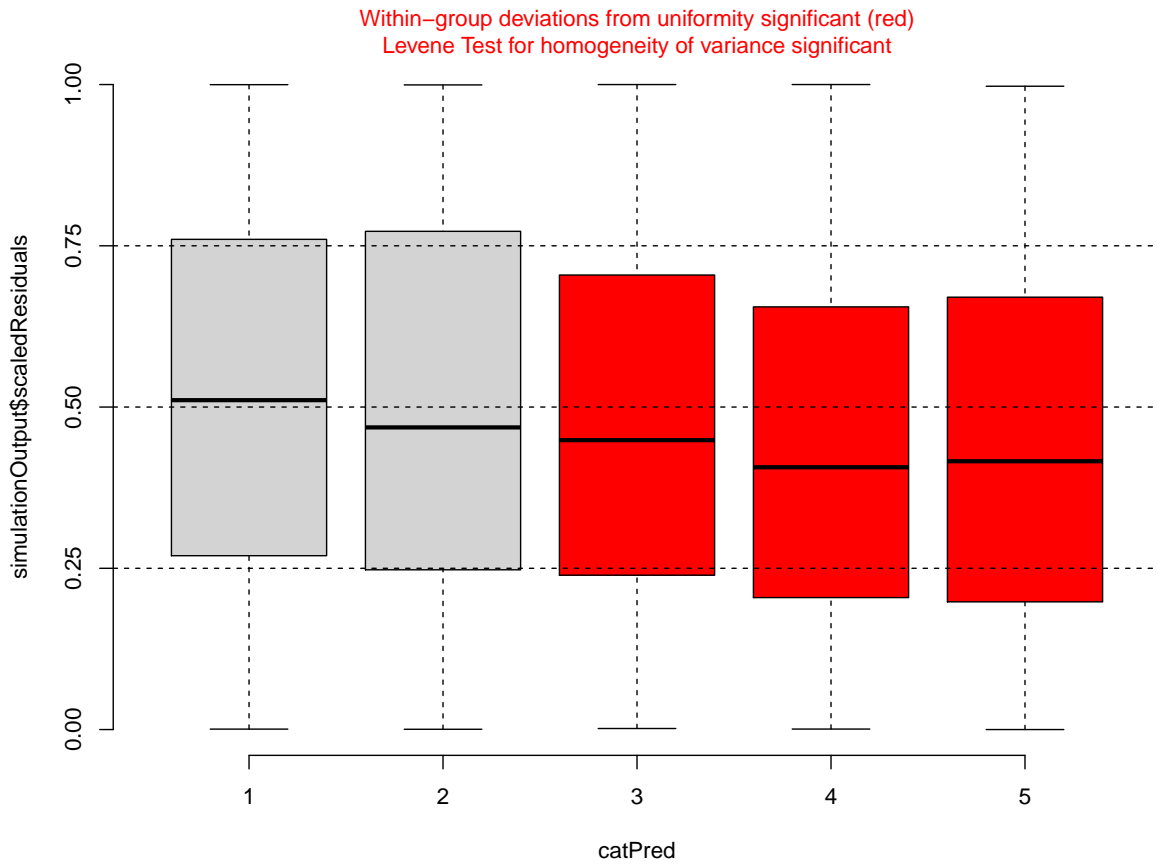
There is a slight deviation from a perfect uniform distribution as it can be seen by the fitted quantile regression line (dashed red line), but it seems small and without a systematic pattern.

Counting method



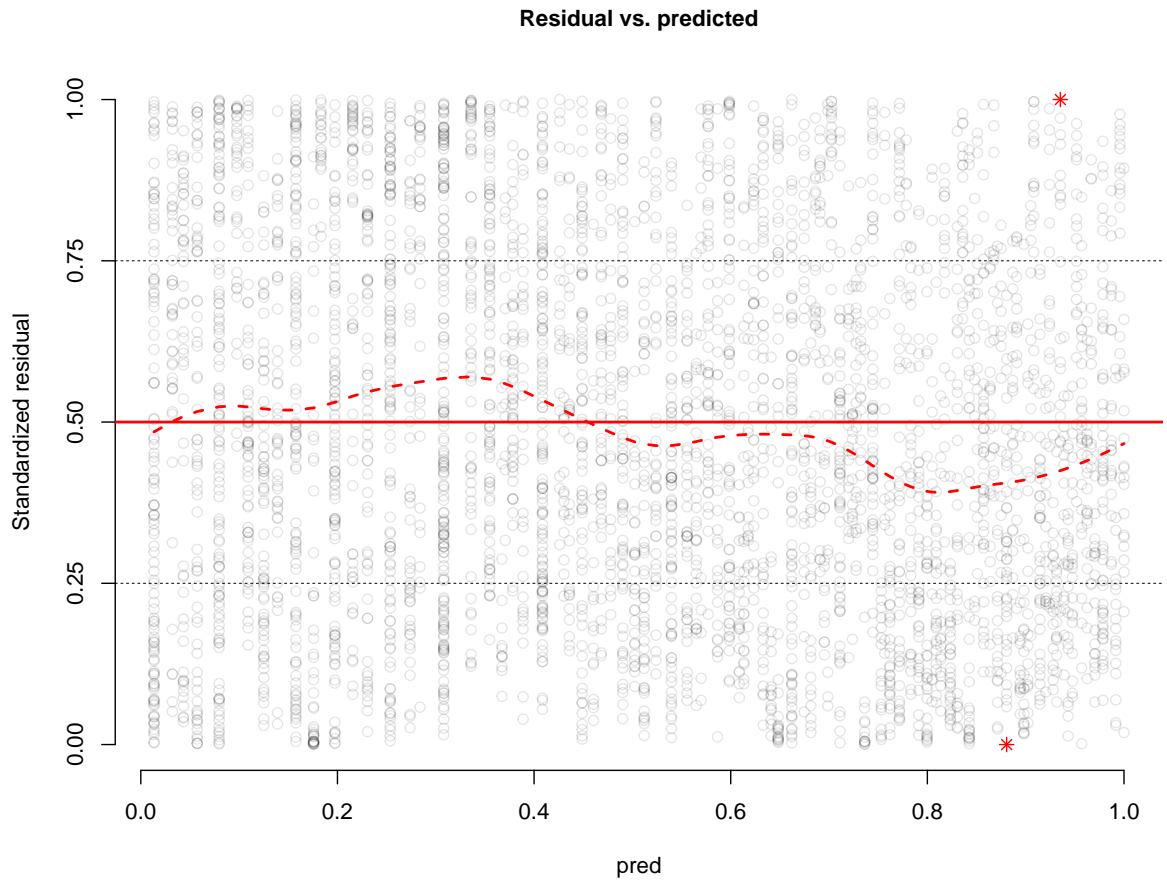
There is a statistically significant deviation from the uniform distribution for the quick count and the unlimited count (count_30s and count_1m, respectively), but the box-whisker plot shows that this deviation is very small.

Experience in botany



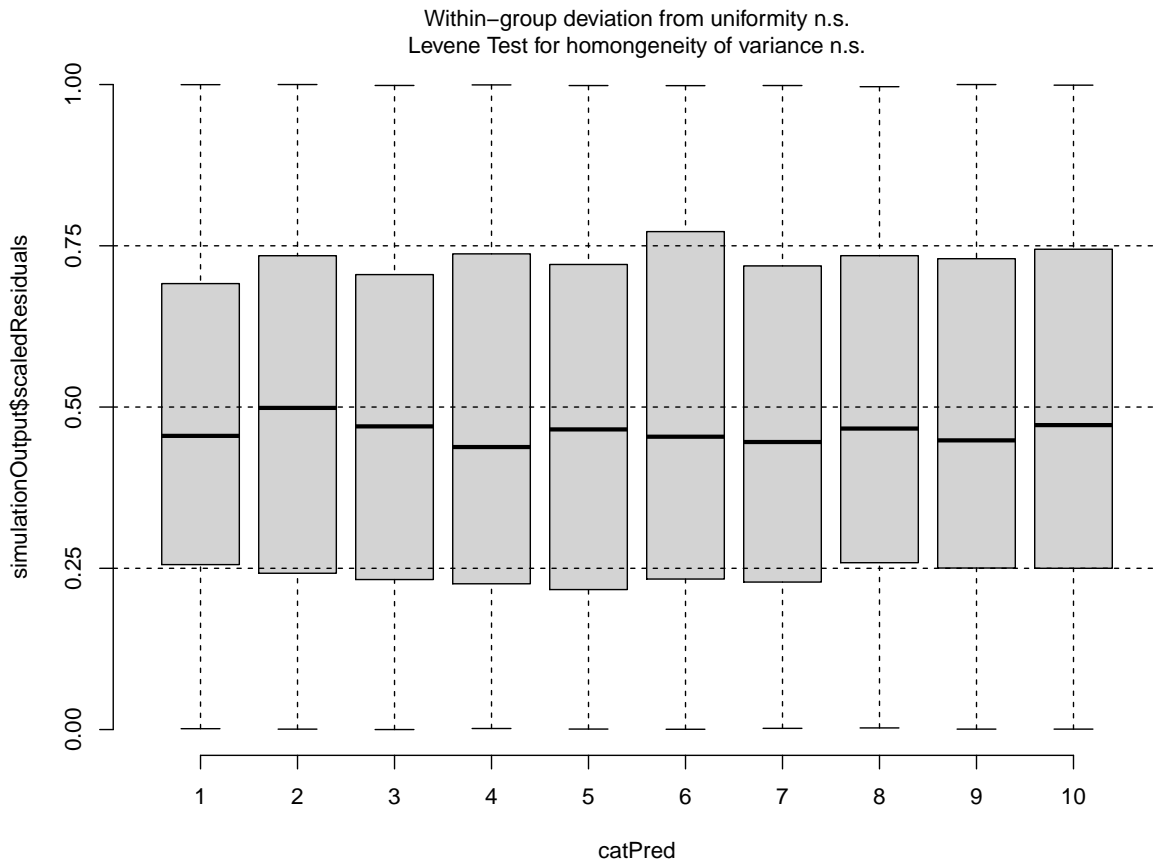
As for the counting methods, there is a deviation for the experience levels in botany 3, 4 and 5. There could be a systematic pattern here (deviation increases with the level in botany), but the deviation is very small, so it seems there is nothing to worry about.

True density of individuals



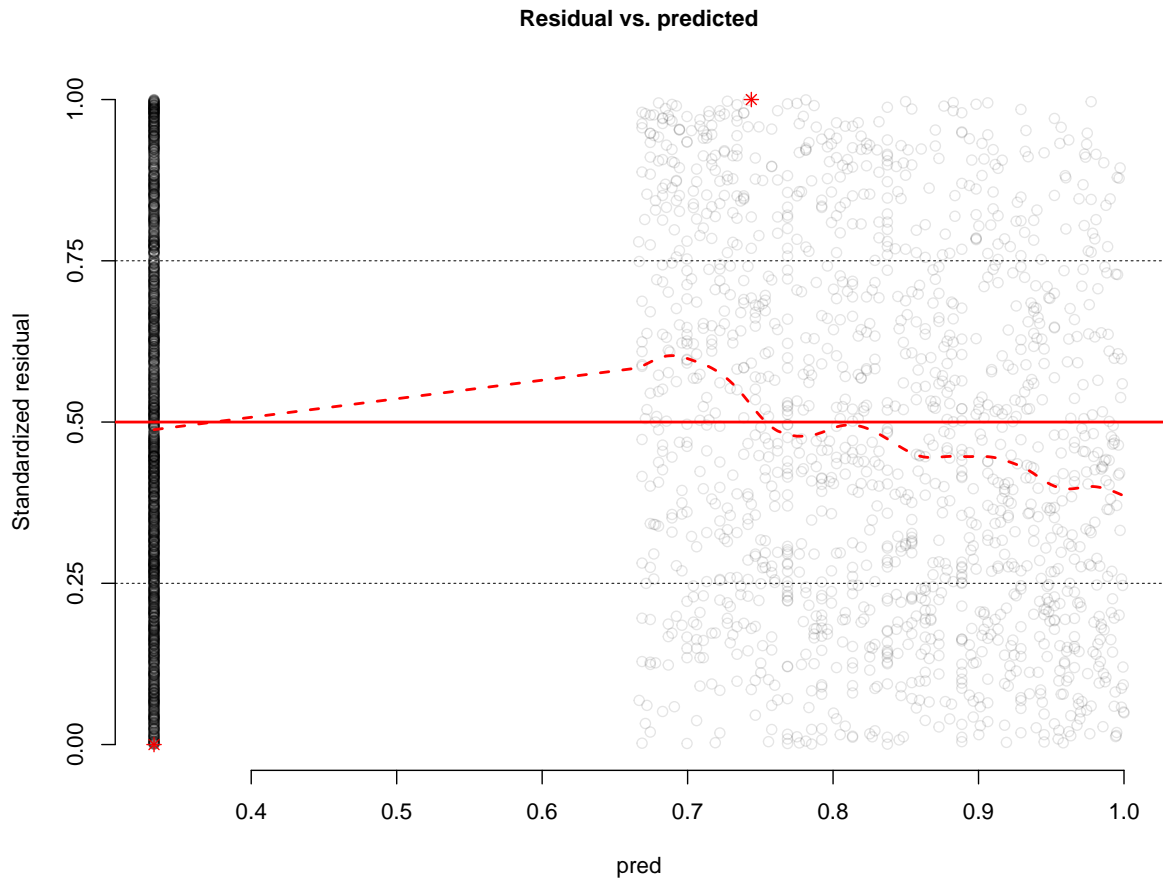
The fitted quantile regression finds a significant deviation but it's very small and no pattern can be seen in the residuals.

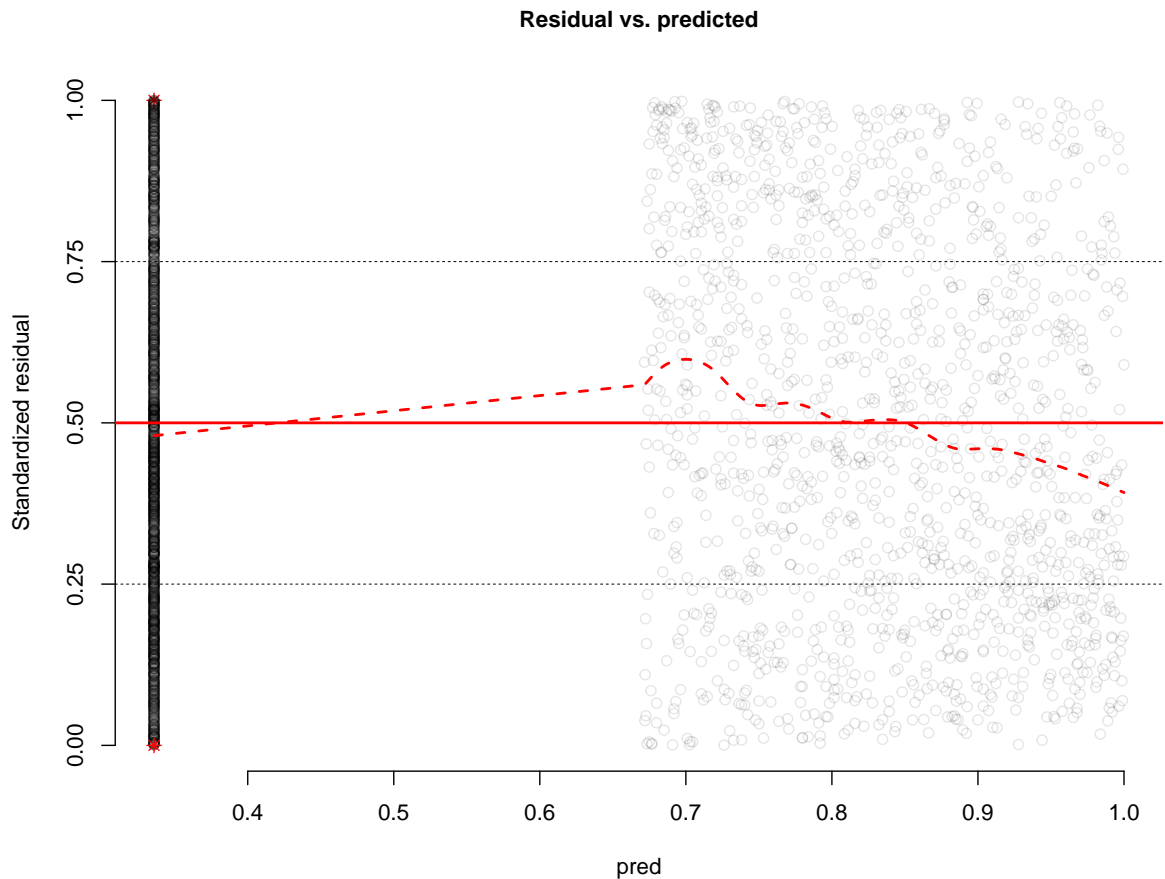
Quadrat order



There is no deviation from the expected uniform distribution.

Counting time





For the two plots above, the strange pattern in the residuals (no points in the left half of the plots) comes from the fact that we had to code manually the two counting time variables, as for one of the three counting methods the counting time was fixed at 30 seconds and not variable as it was for the other two methods. We created two separate variables (`counting_time_1m` and `counting_time_cells`), which contained the recorded counting times for the unlimited count and the cell count, respectively. For the rows of the dataset concerning the other counting methods, the values of these two variables were set to zero. Thus, only the right part of the plots have to be interpreted here, and there seems to be no clear pattern in the residuals in this part of the plots.

References

- Florian Hartig (2022). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6. <http://florianhartig.github.io/DHARMA/>
- Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Alaguela, H., Teplitsky, C., Réale, D., Dochtermann, N. A., Garamszegi, L. Z., & Araya-Ajoy, Y. G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution*, 11(9), 1141–1152. <https://doi.org/10.1111/2041-210X.13434>

Appendix 6: Coefficients of the model

All predictors were standardised before fitting the model. The model fitting function (using the R package lme4) is below:

```
mod_final <- glmer(prop_detect ~ (1|species) + (1|species:quadrat_id) + (1|obs_id)
  + species_conspicuousness * habitat_closure
  + species_conspicuousness * counting_method
  + habitat_closure * counting_method
  + exp_bota * counting_method
  + count_TRUE * counting_method
  + quadrat_order * counting_method
  + counting_time_1m * habitat_closure
  + counting_time_1m * species_conspicuousness
  + counting_time_cells * species_conspicuousness
  + counting_time_cells * habitat_closure,
  family = binomial, data = df_3_methods, weight = count_TRUE)
```

Table S6.1: Fixed effect coefficients of the selected model.

term	estimate	std.error	conf.low	conf.high	statistic	p.value
Intercept	-0.0047	0.1684	-0.3347	0.3252	-0.0281	0.9776
Species con- spicuousness	0.2103	0.1716	-0.1260	0.5467	1.2257	0.2203
Habitat closure	-0.3102	0.1050	-0.5159	-0.1045	-2.9552	0.0031
Method [unlimited count]	0.4256	0.0199	0.3866	0.4646	21.3750	0.0000
Method [cell count]	0.8436	0.0254	0.7938	0.8933	33.2091	0.0000
Experience botany	0.0595	0.0358	-0.0106	0.1295	1.6630	0.0963
Density	-0.2907	0.0488	-0.3864	-0.1949	-5.9519	0.0000
Quadrat order	0.0127	0.0082	-0.0035	0.0288	1.5381	0.1240
Counting time x Method [unlimited count]	0.2088	0.0085	0.1921	0.2254	24.6281	0.0000
Counting time x Method [cell count]	0.4790	0.0120	0.4555	0.5026	39.8179	0.0000
Species con- spicuousness x Habitat closure	0.1430	0.0911	-0.0356	0.3216	1.5694	0.1166

term	estimate	std.error	conf.low	conf.high	statistic	p.value
Species conspicuousness x Method [unlimited count]	0.0685	0.0268	0.0159	0.1210	2.5541	0.0106
Species conspicuousness x Method [cell count]	0.0348	0.0325	-0.0290	0.0986	1.0702	0.2845
Habitat closure x Method [unlimited count]	-0.1246	0.0204	-0.1646	-0.0845	-6.1021	0.0000
Habitat closure x Method [cell count]	0.1279	0.0230	0.0829	0.1730	5.5639	0.0000
Method [unlimited count] x Experience botany	0.0637	0.0112	0.0417	0.0857	5.6836	0.0000
Method [cell count] x Experience botany	0.2072	0.0123	0.1831	0.2313	16.8792	0.0000
Method [unlimited count] x Density	0.0237	0.0093	0.0054	0.0420	2.5389	0.0111
Method [cell count] x Density	0.0275	0.0109	0.0062	0.0488	2.5351	0.0112
Method [unlimited count] x Quadrat order	0.0641	0.0114	0.0418	0.0864	5.6414	0.0000
Method [cell count] x Quadrat order	0.0903	0.0122	0.0665	0.1142	7.4255	0.0000
Habitat closure x Counting time x Method [unlimited count]	-0.0221	0.0095	-0.0407	-0.0035	-2.3266	0.0200

term	estimate	std.error	conf.low	conf.high	statistic	p.value
Species conspicuousness x Counting time x Method [unlimited count]	0.0068	0.0096	-0.0120	0.0257	0.7091	0.4782
Species conspicuousness x Counting time x Method [cell count]	0.0513	0.0117	0.0284	0.0742	4.3962	0.0000
Habitat closure x Counting time x Method [cell count]	-0.2045	0.0091	-0.2222	-0.1867	-22.5880	0.0000

Table S6.2: Random effect standard deviations and variances of the selected model.

term	SD	variance
species:quadrat_id	0.6474	0.4191
obs id	0.3989	0.1592
species	0.7650	0.5852

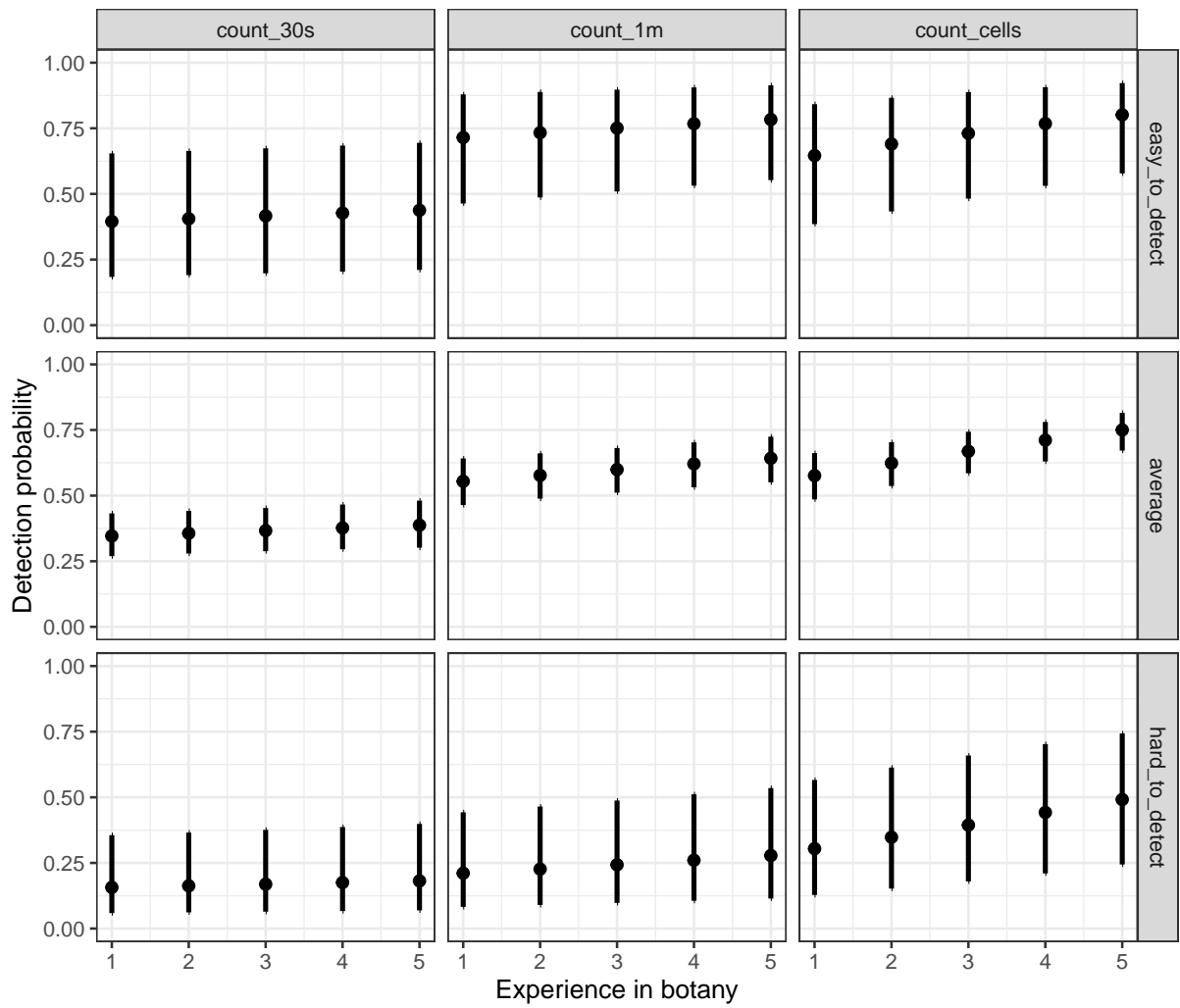


Figure S6.1: Predicted detection probability depending on the level of experience in botany of the observer in easy detection conditions (species conspicuousness = 4; habitat closure = -1.5), average conditions (species conspicuousness = 2.5; habitat closure = 0.5) and difficult conditions (species conspicuousness = 1; habitat closure = 2.5). Only the values in average conditions are used in the main text.

Appendix 7: Results with excess detections reduced to 100% detection

The three figures below are the alternative versions of Figs 2–4 from the main text, made by fitting the model to the dataset in which the excess detections were set to a 100% detection rate instead of removing them from the dataset. The differences are imperceptible, which indicates that the excess detections did not play a role in the analysis results.

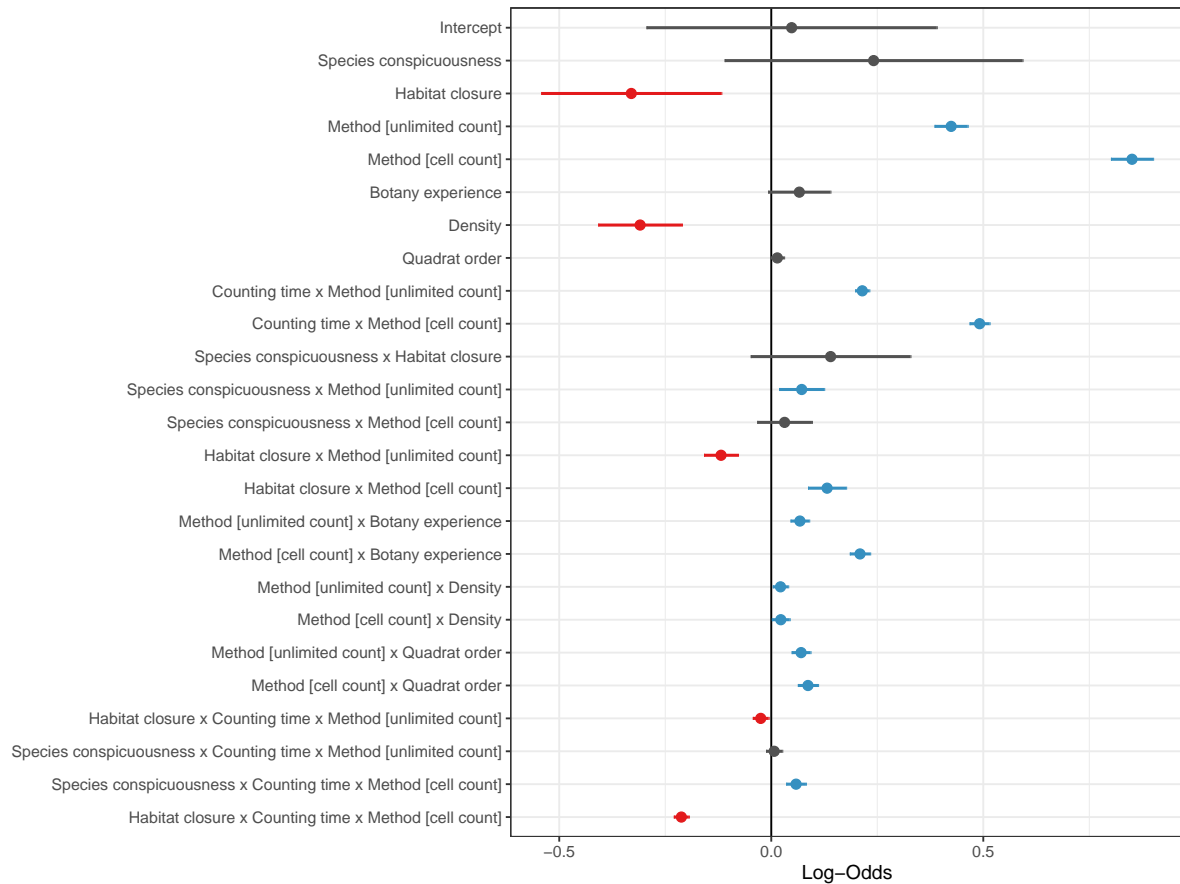


Figure S7.1: Coefficients of standardised variables in the selected model. Dots represent estimated coefficients, and lines represent 95% confidence intervals. Positive coefficients (blue) indicate that when the variable increases, the proportion of detected individuals increases, while negative coefficients (red) indicate the opposite. Coefficients with a non-significant effect are shown in grey. For the variable ‘counting method’, the reference level is the estimate of the number of individuals in 30 sec. The coefficients presented for the other two methods indicate the difference in mean detection rate obtained with those methods compared to the reference level.

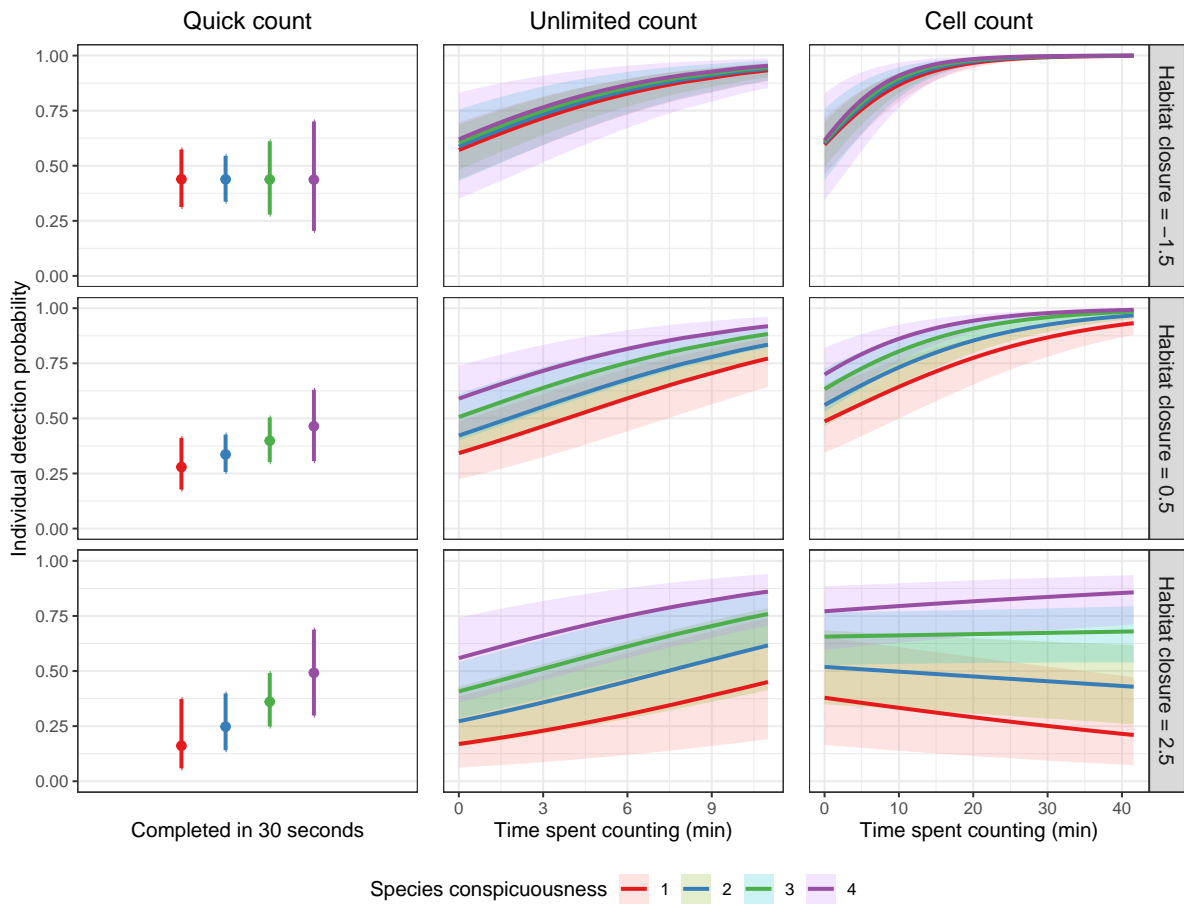


Figure S7.2: Predicted detection probability of individuals depending on species conspicuousness, habitat closure, counting time and the counting method used. The other variables included in the model are held constant at the following levels: $\text{exp_bota} = 2.5$, $\text{count_TRUE} = 100$, $\text{quadrat_order} = 5$. Lines represent the mean proportion of detected individuals, and the shading represents 95% confidence intervals.

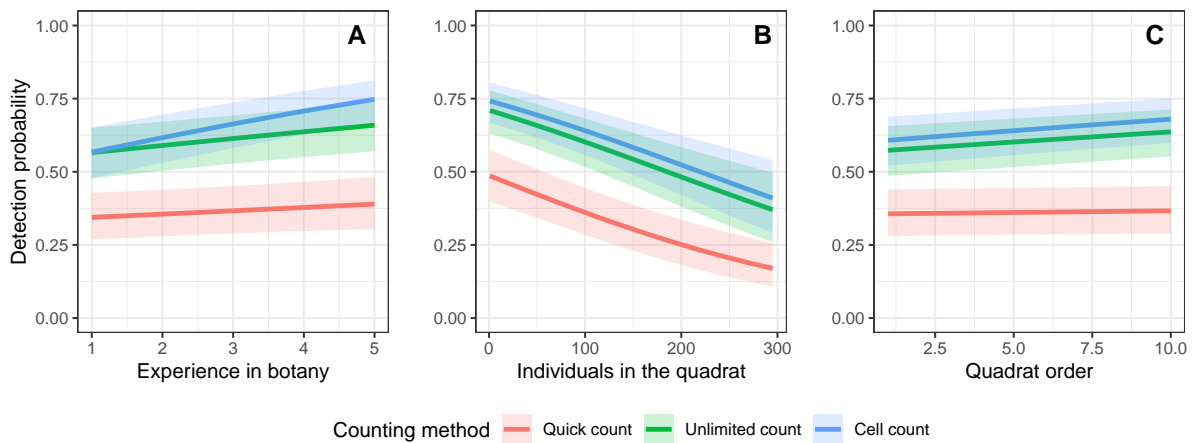
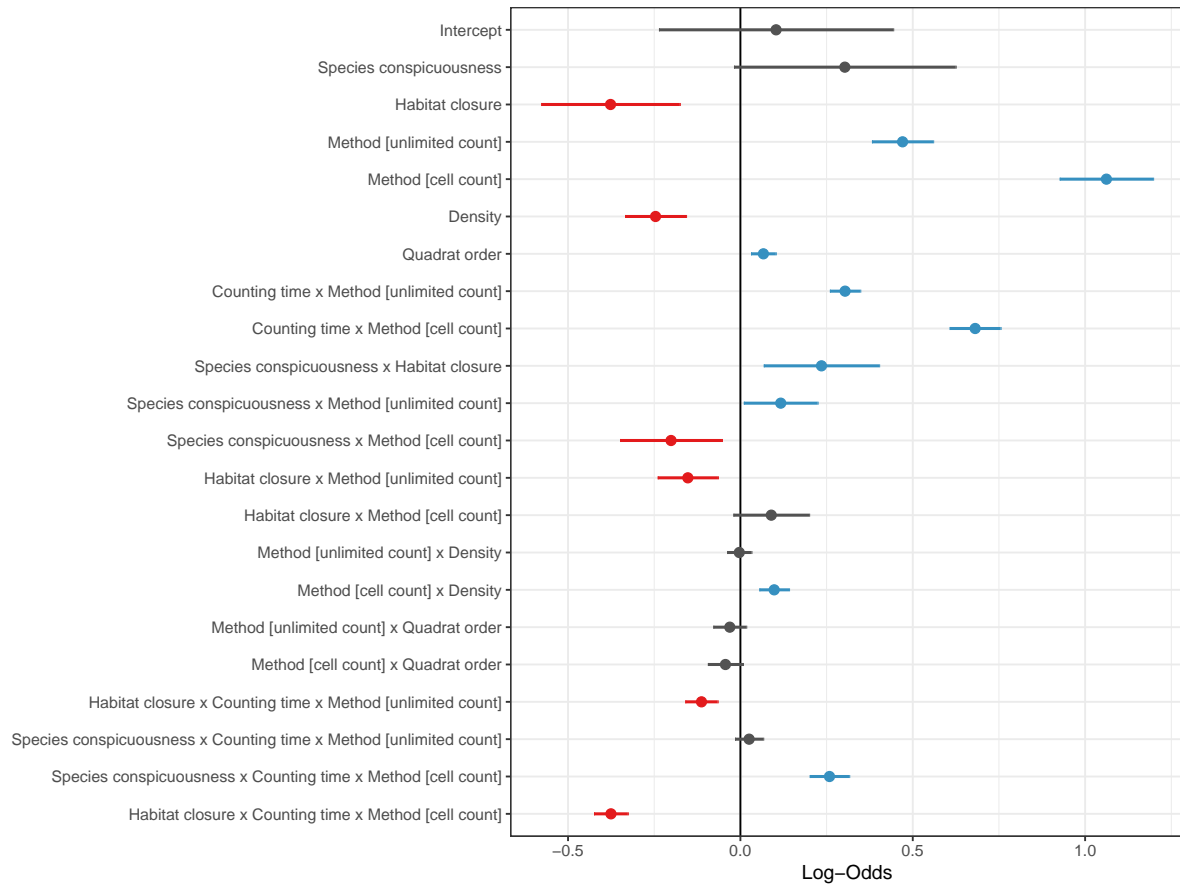


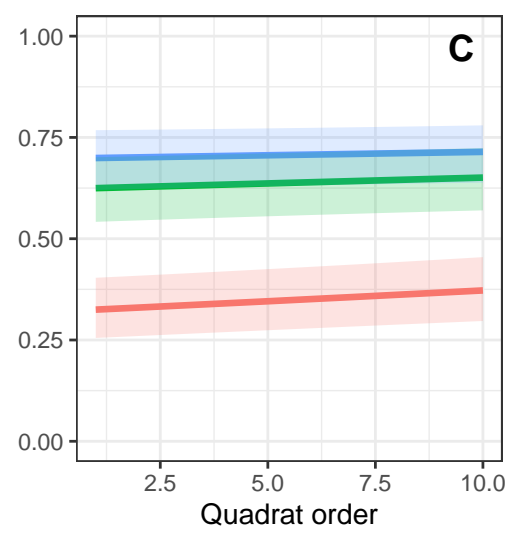
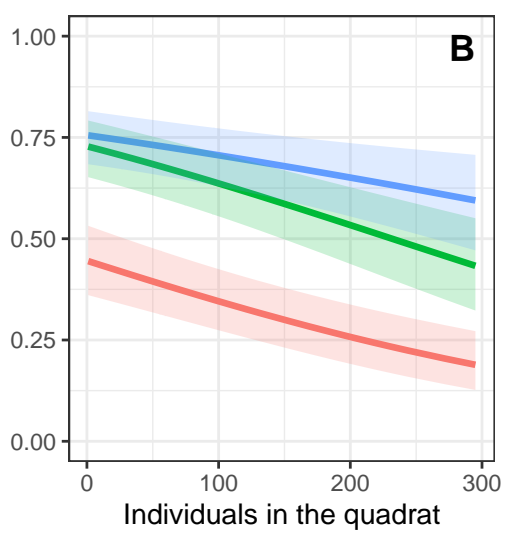
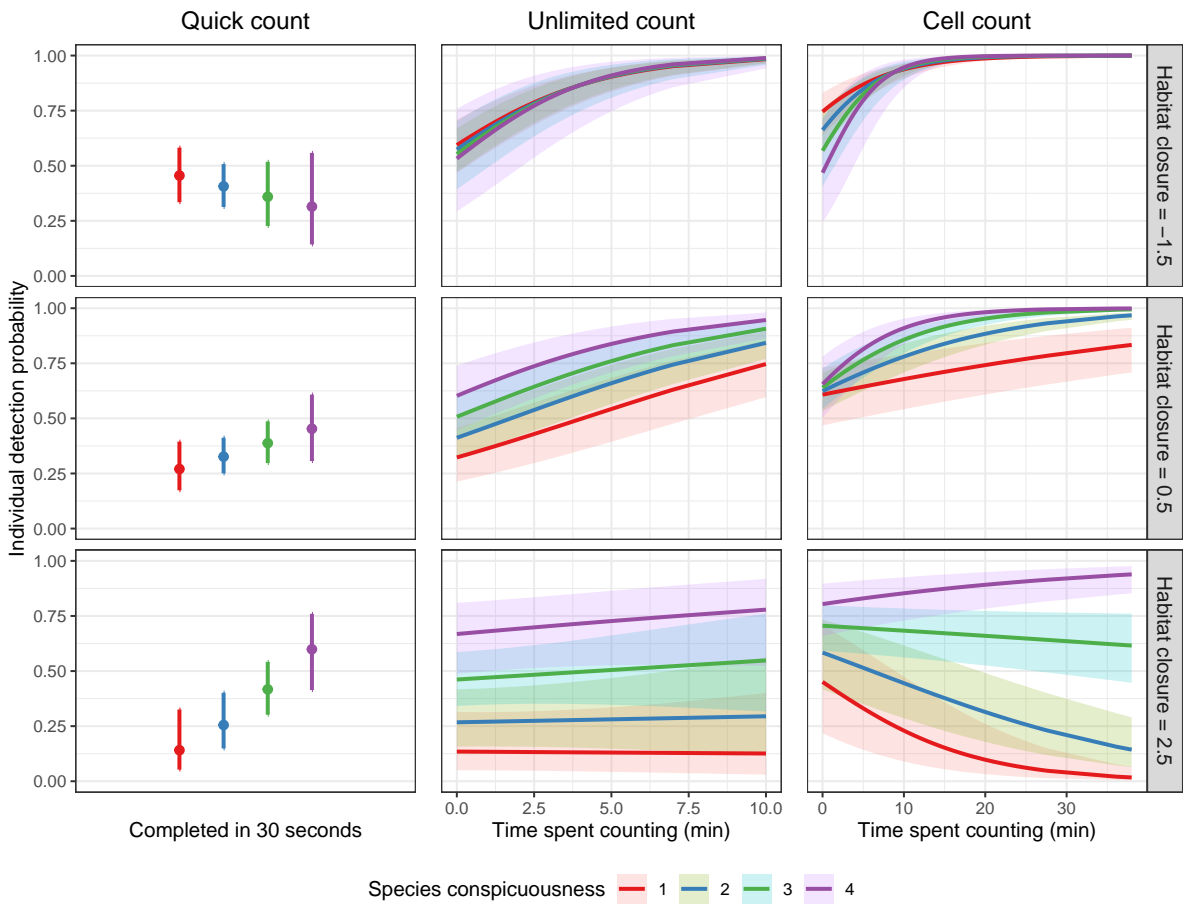
Figure S7.3: Predicted detection probability of individuals depending on the experience in botany of the

observer (A), the true density (B) and the position of the quadrat in the round (C). The other variables included in the model are held constant at the following levels: species conspicuousness = 2, habitat closure = 0, quick count time = 0.5 min, unlimited count time = 3 min, cell count time = 3 min. Lines represent the mean detection probability of individuals, and the shading represents 95% confidence intervals.

Appendix 8: Results with only the experienced botanists

The three figures below are the alternative versions of Figs 2–4 from the main text, made by fitting the model to a version of the dataset where only the observers with a high level of experience in botany were kept (i.e. levels of experience of 4 and 5 out of 5). This reduced the number of observations in the dataset from 4319 to 1070. This resulted in substantial differences in the parameter estimates and in the model's predictions, but the general pattern of the predictions was unchanged. This indicates that our results are not due to an excess of observers with little or no field experience in our sample of observers.





Counting method — Quick count — Unlimited count — Cell count

Appendix 9: List of the participants

We would like to warmly thank the following 167 volunteers who participated in the experiment, some of them multiple times, including during the preliminary tests:

ALBERT Christophe, ALEGOT Bastien, AMARA Juliette, AMBROSIO DE LA IGLESIA Raquel, ANDRIEU Frederic, ARGAGNON Olivier, ARNAL Gerard, ARNAL Veronique, ASSIO Cindy, ASTRUC Guillaume, AUFFRAY Thomas, AUTHIER Louise, BARCZI Jean-Francois, BARRY Pierre, BASSIBEY Arnaud, BASTIEN Marion, BEAUTRU Lucas, BELGHALI Soumaya, BELLANGER Jean-Michel, BENVENEGNEN Ulysse, BERNARD Charles-Etienne, BIOSSE Guilhem, BLANQUART Audrey, BLAYA Romane, BLIN Mirham, BLONDEL Francois, BONNET Lucie, BOULINIER Jenna, BOULY Ilona, BOUVIER Elodie, BRENDDEL Frederic, BRIERE Maxime, CADET Serge, CANONNE Coline, CHAMBRELIN Justin, CHATELLIER Cyllene, CHAULIAC Christophe, CHAYRIGUES Sarah, CLOUET Louis, COCHENILLE Thomas, CONTOURNET Pascal, COULON Mireille, COUTURIER Thibaut, CUBAYNES Sarah, DARONAT Maelys, DE FRANCE Arthur, DECOMBEIX Anne-Laure, DECROCK Roxane, DELMOND Mathilde, DELPORTE Etienne, DEMONGEOT Marilou, DENIS Nans, DENTANT Cedric, DESPLANQUE Carole, DESPLAT Morgane, DIXON Lara, DORTEL Emmanuelle, DUBUISSON Candice, DUCRETTET Juliette, DUPUY Solene, DURRET Cassandra, ENGEL Julien, ESSELIN Mathilde, FALLOUR Delphine, FAUCHE Marine, FAURE Karine, FELIX Lila, FERRAILLE Thibaut, FERRER-LABROCHE Sophie, FICHTER Marc, FINOCCHIANO Marie, FLACHER Floriane, FONTAINE Ninon, FONTES Hugo, FORT Noemie, FORTUNY Xavier, FOUQUART Marilyne, FRAYSSE Remi, GANAULT Pierre, GAUTHIER Perrine, GENIEZ Philippe, GEOFFROY Sabine, GILBERTAS Lauriane, GILLIOT Marianne, GIRARDIER Marion, GRILLAS Patrick, GRITTI Clara, GUIRAUD Elise, HENRY Etienne, HOLVECK Pascal, HOPKINS David, HUYNH TAN Bernadette, ICARDO Emmanuel, IMBERT Eric, JANIN Romain, JEANNOT Anne, KACAMAK Begum, KANDEL Margot, KELLER Johann, KLESCZEWSKI Mario, LABROCHE Aurelien, LAQUEVILLE Manon, LARCHEY Enola, LARRE Antoine, LATRON Mathilde, LAUGIER Fanny, LAURET Valentin, LE BERRE Maelle, LE BORGNE Elsa, LEFRANCOIS Olivier, LLORENTE ZUBIRI Lucia, LOURENCO Marion, LUKAS Marie-Lou, MACE Bastien, MARQUES Fabien, MARQUIS Alois, MARRE Jacques, MARRE-CAST Josette, MASSART Pablo, MATUTINI Florence, MAUCLERT Virginie, MAURER Gilles, MEINER Eric, MERTENS Louis, MEYER-BERTHAUD Brigitte, MIGAIROU Juliette, MOLINA James, MOLINO Jean-Francois, MUNZINGER Jerome, NACIRI Marwan, NADOT Sophie, PARIS Celia, PECHEUR David, PEROT Clara, PETIT Christophe, PIRES Mathias, POIRIER Clara, PONS Aurelia, PONS Virginie, POPOVITCH Yannick, POURTIER Laure, PRIEUR Jean, QUEDREUX Soham, ROCHER Leo, ROCHWERGER Naemie, ROLLIER Christophe, ROSSI Sofia, ROUYER Marie-Morgane, SAATKAMP Arne, SABY Lea, SAUVAJON Lou, SAVIO Laura, SEVIN Claire, SIMONNET Franck, TCHILINGUIRIAN Julien, TEMOIN Jean-Luc, TERREAU Alexandre, TESTUD Guillaume, TON Louis, TURPIN Louise, VELA Errol, VIDALLER Christel, VINCENT Gaelle, WASELLA Tatiana, YAVERCOVSKI Nicole, ZANELLA Agathe.