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Review of the PhD thesis 'The role of the brown bear *Ursus arctos* as a seed disperser: a case study with the bilberry *Vaccinium myrtillus*' by candidate Alberto Garcia-Rodríguez at the Institute of Nature Conservation of the Polish Academy of Sciences.

The thesis presents an in-depth analysis about the role of brown bears and sympatric birds and mammals as endozoochorous plant seed dispersers of bilberry. The candidate and his team thereby address and merge (at least) two important ecological questions. First, Alberto and his team quantify the Seed Dispersal Effectiveness for bilberry by brown and other wildlife. This is important from an ecological and conservation perspective, because it informs the public about the ecological roles of individual species and their complementarity in providing ecosystem services such as plant seed dispersal. Several important dispersers such as the brown bear and the red fox have been persecuted by humans throughout history. Such persecution does not 'just' remove individuals or populations, it also takes away the important ecosystem services such species provide. Second, the focal plant species is bilberry, a keystone species in Eurasian boreal and temperate forests. The mating system of bilberry is still not very well understood and has been considered as a 'reproductive paradox' for several decades. The species produces vast amounts of viable plant seed on an annual basis, but their seedlings are rarely found in the wild and reproduction occurs predominantly clonal. Alberto and his team show that this actually no such a paradox: bilberry seedlings are in fact very common throughout the landscape at locations where wildlife deposit bilberry seeds through endozoochory. The seedlings are especially common at microsites suitable for bilberry germination and establishment, such as bear beds and decaying wood. The same mechanism may apply for other berry producing species with a similar mating system as well. Overall, the brown bear seems to play a pivotal role in bilberry dispersal, and the species may have a similar role for other berry producing species throughout its entire range.

The thesis is a solid piece of work and combines literature review, meta-analyses, experiments, extensive fieldwork, genetics, statistical modelling, patience, and thinking hard. The thesis is well written, understandable, and concise (sometimes perhaps a too concise), and is proof that the candidate has a mature understanding of the topic and masters the scientific method. The thesis is a collection of one published scientific article and three manuscripts submitted or in preparation for submission. I have no doubts that the three manuscripts will be published in the near future. The four papers are preceded by a very short introduction and followed by a brief short conclusion.

Introduction - The introduction provides a concise background and is overall very relevant for the thesis. The author addresses key concepts that recur throughout the thesis, such as the Seed Dispersal Effectiveness framework (Schupp et al. 1993, 2010), quantitative and qualitative aspects of endozoochory, seed shadows, and long distance dispersal. The brief theoretical background is (logically) followed by a description of the study species, i.e. the brown bear and the bilberry. The species descriptions are sufficiently informative for the purpose of the PhD thesis and include concepts such as recruitment windows of opportunity, the megafauna concept, the annual cycle of brown bears, etc. The study area description is also sufficiently informative, and contains information about sympatric birds and mammals relevant for the study as potential seed dispersal agents. The study area description concludes with two potentially very important concepts in terms of endozoochory; i.e. human activity and supplementary feeding. The final section of the introduction comprises the objectives of the thesis, which are presented very concise and as rather descriptive goals.

Several of the concepts that are mentioned in the introduction could have used more background and context for making the introduction more informative, especially for the non-biologists among us. For example:

- Why and how are human activities and supplementary feeding potentially important factors that can affect endozoochory? (p23)
- In the objectives for paper I, it is stated 'I also explore factors related to brown bear's biology and ecology that may influence their effectiveness as seed dispersers'. It would have been helpful to be explicit here and state which factors will be explored and why. (p24)
- The fourth aim of paper III states that the author will investigate which of the Seed Dispersal Effectiveness components ('quality' or 'quantity') is the better surrogate for the total SDE of the different bilberry dispersers. This sentence suggests that the SDE framework could use improvement for becoming a more easily applicable method or framework to investigate and compare SDE of different dispersers. As a reader, this methodological aspect comes a bit out the blue and could use more context. What is the background for exploring this? (p24)

It is a fine balance to write concise and complete. I feel that the author managed to do this in several parts of the introduction, but perhaps presented other sections somewhat too concise.

Paper 1 (published in Scientific Reports) – This paper addresses a qualitative and a quantitative aspect of the SDE framework, i.e. the occurrence/proportion of fleshy fruits in brown bear diet across their entire range, and the effect of gut passage on seed germination in a number of selected species of central Europe. The article has three main findings. First, fleshy fruits are an important part of bear diet throughout their range. In total, 101 different species occur in brown bear diet, which comprises about 24% of food all items (26% volumetric). Rubus and Vaccinium were the most important genera in brown bear diet globally. Second, some variation in the importance of berries in bear diet exists across biomes, and third, that gut passage enhances germination in several species.

In the paper, is it concluded that the brown bear is a legitimate megafaunal seed disperser. The definition (as presented in the paper) states that a legitimate seed disperser is a mutualistic agent that combines high quality and quantity in terms of seed dispersal, and has a strong impact on the regeneration process and population dynamics of the dispersed plant

species. The analyses (and some additional field data) suggest that bears indeed disperse considerable amounts of plant seed and that ingestion may facilitate germination in some species. However, the paper does not present data on actual regeneration and population dynamics of the dispersed species and, as such, the conclusion is perhaps too strong given the result in this particular paper.

- What kind of data would you ideally collect for identifying if certain species qualify as legitimate seed dispersers? How would you design such a study?

The introduction of this paper is well written and to the point. However, I wonder about the feasibility of aim 1; i.e. to identify all fleshy-fruited plant species eaten by brown bears worldwide.

- How was this done and when can one conclude to have identified all? (p33)

Overall, the methods section was not very clear to follow, and I missed bit the justifications for certain decision. For example:

- For the literature review, when was a study considered as 'relevant'? (p34)
- Why were the first 1000 hits selected instead of refining the search? (p34)
- How was a study population defined? Does only including the latest study in one specific area avoid pseudoreplication in the dataset? (p34)
- There seems to be a cluster of studies in Japan (Hokkaido, 11 studies) and in Poland/Slovakia (5 studies) (see Figure 1, appendix S6). Could the studies included in these clusters not be considered as pseudoreplication and thereby affect the results? Could you account for this in the statistical analyses?

Results - The descriptive statistics and the NMDS appear to be very powerful and convincing to analyze the biome data. The NMDS stress value also indicates a good model fit and the NMDS1 is a clear indication for a 'biome gradient', which is also supported by the permanova test. This is really convincing. The GLMs on the other hand, are less convincing, with an intercept (Montane grasslands and shrublands) that is always significantly different from 0, but no biomes being significantly different from the intercept (Appendix S2).

- Based on the GLMs, how important was the biome effect really on the number of genera, species, and the relative frequency of occurrence of fleshy fruits in bier diet? Have you contrasted these models against a null model?
- Table 1 shows small superscript letters to indicate statistical significance between the biomes, indicating that some kind of posthoc test has been used. How was this evaluated (does not seem to be reported in the methods)?

About the quality aspect – figure 3 and especially Appendix S5 speak for itself: depulped and seeds that passed the digestive system of bears germinate better than seeds in entire fruits. I realize that the PhD candidate was not involved in the practicalities and design of this experiment, and I will not further elaborate on this aspect.

Apart from a perhaps too strong conclusion given the data, the discussion is mature and a good refection of the work in a broader ecological context. Strong points here are the reference to herbivorous megafauna, habitat loss and population declines and potential impacts on zoochory as an ecosystem service, and the acknowledgement that post dispersal

stages need to be investigated to fully understand the qualitative aspects of brown bears (and other species) and SDE. However, a major part of the data analyses is attributed to analyzing variation in the number of species and genera of fleshy fruits dispersed and the frequency of occurrence of fleshy fruits in bear diet across biomes. This has been addressed only very briefly in the discussion.

- From an ecological perspective – what does it really mean that there is (no) variation in these factors among biomes?
- Bears have been removed from large parts of their original range. How do you expect will the genetic variation of fleshy fruits be in those areas compared to the genetic variation of these plants within the current bear range? Could other mechanisms 'replace' bears?

I would like to refer to two publications that can be relevant for this study:

Harrer, L. E. F., and T. Levi. 2018. The primacy of bears as seed dispersers in salmon-bearing ecosystems. Ecosphere 9(1):e02076. 10.1002/ecs2.2076

Albert, T., Raspé, O., and Jaquemart, A.-L. 2004. Clonal diversity and genetic structure in Vaccinium myrtillus populations from different habitats. Belg. Journ. Bot. 137 (2): 155-162 (2004)

Paper 2 (submitted to Biological Conservation) – In this article, the authors use genetic techniques to investigate the diet of brown bears in the Tatra National Park, with a special focus on the importance of fleshy fruits in the diet (i.e. a quantitative aspect of SDE). The authors use diversity metrics to investigate diet variation in relation to season and month, and discuss the results in a context of human disturbance. The article is mostly descriptive and is complementary to the findings in paper 1. The main conclusion of the paper is that despite a high level of human disturbance, bears still seem to play a key role as seed dispersers in the study area. The conclusion might be somewhat overstated because the human effect on diet has not really been evaluated in this paper (see Elfström et al. 2014 for a good example), and because we don't know (yet) the position of bears in the SDE landscape relative to other dispersers.

The introduction is short and to-the-point and raises ecologically potentially very important questions – how does human disturbance, including supplementary feeding and resource extraction influences ecosystem services such as endzoochory. The paragraphs on diet and genetic tools for diet studies, as well as the section on study species and how human activities may alter seed dispersal are very well written and clear. This section ends with the statement (p85) 'However, the impact of human activities of the diet of brown bears and their role as seed dispersers is poorly understood'. This statement is what I consider as the main focus or problem statement of the paper (which is, in my opinion, a very important one!). However, I don't think that the specific objectives really contribute to answer that question. Stating specific and realistic research questions that can be answered using empirical data could help to better tie research questions to the overall objectives.

- Can you explain why dietary diversity and variation therein *per se* are important for the seed dispersal mechanism? (Objective 1, p85).
- Objective 2 states 'How important are fleshy fruits for the brown bear inhabiting the area?'. It is unclear here what is really meant with 'important'. Does that refer to

nutrition, behavior, reproduction, or other things? In addition, how would you define and measure 'importance' here? (p85)

- Similar for objective 3, it is not clear what is really meant with 'providing essential seed dispersal services'. When is something becoming essential (and for what), and how can you measure that?

Methods – Overall, the description of the study area, field data collection, and diet composition identification are clear, well written, and complete [note that '… insects and invertebrates' should be 'insects and vertebrates' if I am not mistaken]. The clarity of data organization and statistical analysis section could perhaps be improved by explicitly stating the response variables and explanatory variables for each model. For example, to model the 'frequency of occurrence' for each taxon suggest that a ratio is used as a response variable, whereas this was actually performed on the individual scat level using presence/absence data.

- You used Poisson regression models to investigate temporal effects in bear diet on the Hill series number. Such models are known to easily produce overdispersion. Have you evaluated this in your study and have you validated the models? (p88)
- There does not seem to be any form of model selection applied here? What is the motivation for this? Could it be meaningful to include null models in the data analyses?

Results – The descriptive results of the diet composition are very well presented and supported by appealing graphics and informative tables. The temporal patterns in the bear diet results are rather difficult to comprehend, even (or especially) from table S6. This table would be more informative if the estimates for all factor levels (2 seasons, 7 months) would be shown and not one summary statistic for each explanatory variable. The estimates would also help to 'give direction' to the results (as is done in paper 1 and 4).

- Table S6 is not a conventional way for showing regression model outputs, which produce estimates for all the factor levels of categorical explanatory variables. Can you explain what the Chi^2, df, and p-value for each model inform us about? (p126)
- The last section of the results clearly describes that fleshy fruits are a substantial part of bear diet during late summer and autumn. Can you think of a statistical test to actually formalize this and complement the descriptive statistics?

Discussion – The discussion is well written and the authors combine addressing the most important findings in addition to some more speculative aspects (e.g. the relation between bears, zoochory, and climate change), which makes it appealing to read. The discussion section is also the arena where one can be speculative (to some extent) and be creative and spark new ideas, perhaps for future research. As in paper 1, I think that some of the statements and conclusions are presented too strong given the data and results. For example, the team demonstrated that berries make up a substantial share of the autumn diet, but not necessarily that these berries are a key resource.

- What is a key resource and has that really been measured here?

In a similar way, it is stated 'We demonstrated that human presence *per se* does not necessarily compromise the feeding requirements [should this not be 'habits' instead?] of brown bears and that the effective and well-informed management is pivotal to guarantee a

natural-based diet in brown bears and the subsequent ecosystem services they provide'. I don't think that these two aspects - human disturbance and management - have actually been demonstrated or addressed. Overall, I think that the discussion could be more convincing if conclusions were expressed somewhat milder.

- What exactly would be the expected compromise be here between human presence and feeding requirements [habits]? (p93)
- This study provides one data point: i.e. a certain bear diet under a given human disturbance regime. If there were to be a compromise between human disturbance and feeding habits – would one not need at least some king of a human disturbance gradient for this (Paper 1 might be a great starting point!)?
- Similar for the management aspect – it is clear from the paper that bears in the study area have a pretty natural diet under the current management system. However, variation in bear diet was not evaluated in relation to different management strategies, and different management styles may not even have an effect on diet. For example, Scandinavian bears are hunted, regularly disturbed, and experience resource competition from berry pickers, but still have a pretty natural diet. Can you explain why exactly the management in your study area is pivotal for a natural diet in bears?

Suggested article:

Elfström, M., M. L. Davey, A. Zedrosser, M. Müller, M. De Barba, O.-G. Støen, C. Miquel, P. Taberlet, K. Hackländer, and J. E. Swenson. 2014. Do Scandinavian brown bears approach settlements to obtain high-quality food? Biological Conservation **178**:128-135.

Paper 3 (resubmission in preparation for Journal of Ecology) – In this manuscript, the authors combine extensive fieldwork, genetic tools, and a germination experiment to quantify the SDE of all members of the community of bilberry dispersers in their study area. The quantity aspect of the SDE framework is measured as the total seed rain (per hectare) for each disperser, whereas the quality aspect is assessed indirectly through a seed germination experiment with seeds extracted from berries and sown on different substrates. The rationale here is that germination rates vary among microsites (vegetation, dead wood, soil, rock) and that dispersal to these microsites varies among dispersers, which the authors also support with data. The manuscript is overall very well written and clear, unique, and presents various important results that will undoubtedly advance our understanding of endozoochory on the landscape and the community level. This has been a massive job!

Introduction – The introduction is clear and to the point. It addresses the overall concept (i.e. complementarity of seed dispersers), the theoretical framework and its common use (i.e. quantity as a better surrogate), and the use and relevance of genetics to identify dispersers. All aspects listed in the research questions are addressed in the introduction. Research questions 2 and 3 are specifically about comparing birds and mammal. For being entirely complete, I think that the introduction could benefit from a short motivation for this choice, and why and how differences between mammals and birds could be expected.

In the paper, one critical assumption is that gut passage does not strongly affect germination rates of bilberry seed, which is very reasonable according to the literature. This allows the team to ignore that aspect in the SDE conceptual framework of Schupp and use 'quality of seed deposition' as the single surrogate for the quality component of SDE. This assumption is

addressed for the first time in the discussion part of the paper. I think it would benefit the manuscript to mention this in the introduction or the methods, because that would free the readers from the idea that gut passage probably has a large effect on seed germination rates and would bias the results.

Methods – Estimating the quantitative component of each disperser was done through the collection of scats along transects. A few methodological aspects arose that were not entirely clear for me or could use some explanation:

- Were exactly the same transects searched each time, and were the transects cleaned from scat prior to scat collection in 2017 and 2018? If not, could that potentially affect the results? (p138)
- It also states that all carnivore scats and bird droppings were collected within each transect. I assume that scat detection probabilities vary substantially among species and habitat types (e.g. a bird dropping on a stone will be detected relatively easy whereas one on the forest floor could be much harder to detect), which could introduce some bias in the results. Did you test if there was such a bias? (p138)
- If not accounted for variation in detection probabilities of scats, can you think about methods to do so?

In addition to the field sampling, a few modelling aspects were not entirely clear:

- What was the rationale for modeling the seed rain by birds and mammals separately and with different model types (GLMM & GLM)? (p141-142)
- The regression models for the quality component of SDE (seed rain) only considered habitat type interacting with month as the explanatory variables. Why were no other combinations (additive, single effects, null models) considered and could that potentially affect the conclusions? (p141-142)
- The modelling procedure for germination rates of bilberry seed seems to mix two model selection strategies (p-values vs. AIC). The rationale for this is unclear, as well as how the final model was eventually selected. Can you elaborate on that? (p142)

The results are very convincing in terms of seed rain, altitude ranges (perhaps add Figure S5 to the text), the dispersal towards the different microsites by different functional groups, and the SDE landscapes. Figure 2 (p158) also suggest clear temporal patterns in seed dispersal to the different habitat types. Some questions arose about the regression models to assess the seed rain by birds and mammals and in relation to habitat and timing.

- Table 2 does not show the estimates of the different factor levels (and interactions), therefore, it not possible to assess the effect size of the different factor levels from the table. What is the rationale for showing these unconventional tables instead of standard outputs? (p161)
- Furthermore, it is confusing to see the intercept being reported for the GLMMs but not the GLMs. Why was that? (p161)
- For the brown bears in specific, the interaction ‘Timing * Habitat’ and the ‘Timing’ effect appear to be not significant. A p-value of 1 is somewhat suspicious and might indicate that this model did not run very well. Figure 2 suggest very clear patters, and indicate that perhaps some perfect separation or singularity issues came into play? (p161)

- The relationship between germination rate as the response variable and microhabitat and seed abundance as explanatory variables is very clear and interesting (Figure 3a and b), but it would be nice to also see the actual parameter estimates (Table 3). (p162)

Discussion – The discussion is again well written and concise, and addresses the most important findings of the paper. The overall conclusion is that both birds and mammals are important and complementary seed dispersers in space and time, and that the generalists like bears, foxes, and trushes are the most important dispersal agents.

The study has provided quite a bit of food for thought - which is a good thing! In particular, previous studies have found that the gut passage of bilberry seeds by itself does not have a substantial effect on germination. This study shows that the actual deposition habitat also does not have a great impact on the germination rates, but that seed number or density is rather important. This raises the question:

- Would this not imply that endozoochory does not matter and is not important for bilberry recruitment after all?

The statement that the quantity aspect of the SDE framework might be a better indicator for the total effect on plant reproduction compared to the quality aspect is a somewhat counterintuitive, with the two trush species being the most effective dispersers but with an overall much lower dispersed seed number compared to bears, foxes, and martens.

- Could it not be that SDE is positively associated with the quantitative aspect for mammals, but with the qualitative aspect for birds (fewer seeds but in better microhabitats)? Or is the brown bear just an 'ecological outlier' in terms of dispersed seed numbers and thereby biases statistical models and test?

Paper 4 (Submitted to Biology Letters). The overall aim of this study was to demonstrate that recruitment from seed under natural circumstances is common in bilberry, and that it relates to endozoochory. Recruitment from seed in this species has traditionally been considered as extremely rare, and previous research showed that the species (and other related ericaceous species) require 'windows of opportunity' for successful recruitment from seed (RWOs). These windows have been described as small disturbances in soil and vegetation, which are rather moist and nutrient rich. Examples of such RWOs include bear beds, dead wood, uprooted trees, cadavers, etc.

The authors marked scats that contained bilberry seed from brown bears, mesocarnivores, and passerine birds and monitored seedling recruitment at these sites in the subsequent year(s). For the bear scat, the authors monitored paired control sites at various distances from the fecal samples. For a subset of the bear scats, they also monitored survival of seedlings from the year of germination until the following year. The study design and analyzes are appropriate and well performed, and the results are very clear: bilberry seedlings are common and positively associated to frugivore droppings. The abundance of seedlings was higher at bear scats compared to other frugivores, and especially at bear beds. The probability of finding seedlings and their abundance declined with increasing distance from bear scats. Denuded soil (i.e. disturbance) also appeared to have a positive effect on seedling abundance. The title of the paper could not have been chosen better!

Based on these results, the authors also state that they demonstrate that 'repeated seedling recruitment' and not recruitment through RWOs is the main recruitment strategy for bilberry. This is a claim that I think cannot be made given the design, data and results. In fact, in my opinion, the results strongly support that bilberry recruitment is favored by RWOs (see comments to introduction and discussion below).

One small comment to the abstract – It is stated here that the RWO hypothesis for bilberry has not been tested in natural conditions, which is not really the case. A study using genetic techniques (Albert et a. 2004 – see reference provided earlier) found support for the RWO strategy in bilberry. Also, in a closely related species (*Empetrum nigrum*) the role of endozoochory by frugivores in relation to the RWO has been demonstrated (Steyaert et al. 2018).

Introduction – Eriksson and Fröborg (1996) suggest that the hypothetical spectrum of Initial Seedling Recruitment to Repeated Seedling Recruitment can be used as a framework to describe or predict life histories and population dynamics of clonal plants. They postulate that, from a logical point of view, RWO and RSR may be identical. RWO recruitment is by definition a form of repeated seedling recruitment, albeit perhaps at a lower frequency that the RSR extreme of the ISR-RSR spectrum. They also suggest that the continuous RSR strategy would select for seedlings with high competitive quality at the cost of reduced fecundity, whereas the RWO strategy would favor features that enhance the ability to 'find' the windows of optimal conditions for germination and establishment (dispersal attributes like berries). The introduction concludes with the statement: 'Here, we challenge the hypothesis that bilberry seedling recruitment always occurs at very low frequencies in natural conditions and, thus, that the species follows a RWO strategy' (p174)

- This statement suggests that frequencies higher than 'very low' follow a strategy different from RWO. Can you explain this?
- How do you define 'very low'?
- For assessing how 'high' or 'low' the observed frequencies actually are, I think you would need to have some kind of reference levels about what could be expected. If seedling recruitment of bilberry were to be close to the extreme continuous RSR side of the spectrum – how many seedlings per hectare could you expect to establish every year, provided the same fecundity as observed today.

It is stated that 'Still, this hypothesis has never been tested before', which might be a bit of a strong claim. The mechanism of directed endozoochory to RWOs has been tested in closely related species before (crowberry, E. nigrum) (Steyaert et al. 2018). In addition, the paper from Albert et al. (2004) investigates bilberry genetics in a Belgian study system and their results strongly support the RWO strategy for bilberry.

Methods and Results – These sections are overall well written, logic, and clear. Figure 1 and 2 are very clear and informative and Figure S1 and S2 are very illustrative. These supplementary figures show Vaccinnium seedlings, with very small seedlings in the bottom two panels.

- It is not always straight forward to distinguish new seedlings from bilberry and lingonberry, especially not in the field and when there are hundreds of them to inspect. How did you deal with the presence of lingonberry seedlings that were in the

'seedling mix'? The life history and mating system of both species is very similar, so it would not really matter much for the story of the paper if this was not accounted for, but then it would be safer to pool them together as Vaccinium seedlings (seedlings from other Vaccinium species are easier to distinguish).

- Table S2 – there is a p value of 1 here in the Dunn comparison tests. Did that test not converge or run smoothly? (p191)

Discussion – My major comments about the discussion relate back to the ISR and RSR concept and how RWOs and the results fit in there. The first paragraph of the discussion is somewhat contradictive. It is not necessarily because the data shows that seedling recruitment is more widespread than previously expected (according to the literature), that the RWO hypothesis should be discarded. Certainly, recruitment is repeated (but to an unknown rate compared to the RSR end of the spectrum), but it relies on disturbances such as decaying wood or bare soil, which the authors actually find support for in the data here and also in paper 3.

- Back to a previous question – you have now defined the IRS-RSR 'playground'. How do your results fit in and do you consider that high or low?

Also in the discussion, it states that 'This indicates that bilberry recruitment [from seed] is not restricted spatially or temporally', which does not seem to follow logically from the data and results here and in previous studies, because recruitment appeared especially high on suitable substrates such as bear beds, bear scats, and dead wood (spatiotemporal windows) which I would considered as RWOs in the forest floor.

- The results show that recruitment from seed in bilberry occurs much better in disturbances compared to undisturbed vegetation. Does that not provide very strong support for the RWO strategy?

Survival of seedlings have now been investigated on bear scats and for one year. For many of the questions that we pose, it would also be extremely interesting to investigate this also in other microhabitat and over prolonged periods of time.

- What kind of survival rates would you expect for vaccinium seedlings on undisturbed substrate (e.g. mosses) within a stand of adult vaccinium ramets? Would those be higher or lower compared to survival rates at RWOs?

In Scandinavia, we observe that the scats sometimes 'perforate' the forest floor (the moss layer) which may give opportunity for plant seed to establish in these small windows. This appears to be might be a similar mechanism as observed in cadaver decomposition as described by Bump et al. 2009 but on a smaller spatial scale and with scat instead.

- Would you consider scats by itself as disturbances that may function as RWOs?

The seedling detection probability rates reported here are very similar as in our studies in Scandinavia, for both bear beds and random sites (unpublished data). In addition to bird droppings as suggested here, we also sometimes see several seedling emerging directly from a berries that lay on the forest floor. Without any doubt, the seed rain from the parent plants must be substantial but it remains a big question if and how these seedlings survive and make it to an adult.

Steyaert S.M.J.G., Frank, S.C., Puliti, S., Badia, R., Arnberg, M., Beardsley, J., Økelsrud, A., Blaalid, R. (2018) Special delivery: carcasses disperse plant seed towards ungulate carcasses. Biology Letters 14(8):20180388

Bump J.K. Webster C.R. Vucetich J.A., Peterson R.O. Shields J.M. Powers M.D. (2009). Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. Ecosystems 12, 996-1007

Conclusions – The conclusion section is very short and a repetition of the most important findings of the 4 papers. The fifth paragraph briefly mentions how humans can affect endozoochory and the sixth paragraph briefly relates to the ecological role of brown bears as seed dispersers. The conclusion section is surprisingly short and I hoped to find some wild speculations here, follow-up plans, and the most urgent and important questions that you cannot stop thinking about. On the other hand – I totally understand this abrupt ending. You worked very hard for a very long time and now its time to be done with it! Voila – here it is reviewers, take it or leave it! I take it, and I can only congratulate you the amazing piece of work you delivered. But before that – four more questions.

- In Belgium, where I am from, bears have been extinct for almost 8 centuries now. Yet, Albert et al. (2004) showed that the genetic variation of bilberry could be surprisingly high, with up to 21 individuals per 9 m^2 in their study system. Which mechanism do you think could be responsible for this surprisingly high genetic diversity?
- From an evolutionary perspective, bilberry berries seem to be adapted much better for dispersal via birds. The beaks and the berries are a better match for foraging than the berries and the bear's mouth. There is also some evidence that birds detect the black and blue colored berries very well because of their well developed eyesight in the blue and ultraviolet part of the electromagnetic spectrum. It is not really known yet if bears can see UV light. What do you think about this? Birds or bears? And why?
- The apples we grow today in our orchards are a product of natural selection, at least to some extent. The ancestor of our apple comes from the far East and was not larger that a small grape and had a bitter taste. It is believed that brown bears systematically selected for the larger and the sweeter apples and dispersed them through endozoochory, until it became a product of interest for humans and became further cultivated. Should we expect, in a few thousand years to have larger bilberry bushes with very sweet and very large bilberries because of selective foraging and endozoochory by bears?
- What are the urgent and unanswered questions in terms of bears and berries that you can think of?

Overall conclusion

In conclusion, I believe that the doctoral dissertation presented for review, whose author is Alberto Garcia Rodriguez, M.Sc., meets the criteria for doctoral dissertations set out in Article 13 of the Act of 14 March 2003 on Scientific Degrees and Academic Title and Degrees and Titles in Art (Journal of Laws of 2017, item 1789) and in the Act of 20 July 2018, Law on Higher Education and Science (Dz. U. of 2018, item 1668, as amended) and the Act of 3 July 2018, Introductory provisions of the Act - Law on higher education and science (Journal of Laws of 2018, item 1669, as amended). In view of the above, I put forward a motion to the Scientific Council of the Institute of Nature Conservation of the Polish Academy of Sciences

in Krakow to admit mgr Alberto Garcia Rodriguez to further stages of the doctoral dissertation.

In addition, the thesis is of very high quality and I recommend that it should be considered for an honourable mention.

Sincerely,

Sam Steyaert

Sam Steyaert (PhD) [signed electronically]