

Misconceptions about analyses of Australian seaweed collections

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ABSTRACT: One of the greatest impediments to detecting changes in species distributions in response to ocean warming is the lack of baseline data. In a recent article, we compared old (1940–1959) and new (1990–2009) herbarium records of Australian seaweeds and found a net southward shift in the latitude of northernmost collections of temperate species, implying a flora-wide poleward retreat over the past five decades. Huisman & Millar (2013) criticised our methods, contending that a comparison of herbarium records from different time periods cannot be used to infer changes in species distributions without field-based validation. However, our analysis compared the median position of extreme records of random species from random locations rather than focusing on particular species and their possible loss from specific sites. Hence, ground-truthing ‘extinctions’ are of limited value to the interpretation of our analysis. Moreover, subtidal ground-truthing over biogeographic scales is not logistically possible and even runs counter to entire disciplines (e.g. palaeontology, extinction biology and biogeography) that assess hypotheses of extinction and shifting distributions. Huisman & Millar also questioned the direction of biases in the data set. We show here that patterns of collection effort should have produced an apparent shift northward in the absence of a true shift southward. Even if herbaria were not designed for the purpose of detecting species’ range changes, we contend that such collections can contain useful information on the distribution of species across space and time.

KEY WORDS: Climate change, Collection bias, Global warming, Herbarium data, Macroalgae, Range shift

INTRODUCTION

Shifts in species distributions as a consequence of global climate change and long-term climate variability have been observed across all major biomes (Parmesan & Yohe 2003; Sorte *et al.* 2010; Chen *et al.* 2011). Detecting such changes requires knowledge of past distributions, yet such baseline information is rarely available. This is particularly true for the Southern Hemisphere and even more so for marine organisms (Richardson & Poloczanska 2008; Rosenzweig *et al.* 2008). The lack of planned baseline surveys necessitates the use of alternative data sources to quantify species’ past distributions (Sparks 2007; Connell *et al.* 2008).

In a recent article (Wernberg *et al.* 2011), we used a publicly available database (*Australia’s Virtual Herbarium*; AVH 2012) containing electronic herbarium records of Australian seaweeds to test if the most northerly geographical limits of temperate species have shifted poleward over the past 50 years, a period of intense warming in temperate Australia (Pearce & Feng 2007; Ridgway 2007). However,

these findings were recently questioned (Huisman & Millar 2013). Huisman & Millar (2013) did not deny the main thesis of our article – that temperate seaweeds have shifted south – but they did criticise our methods because of ‘an inappropriate interpretation of herbarium records’, ‘the absence of ground-truthing to confirm extirpations’, ‘incorrect interpretation of collection effort’ and criteria for data inclusion. Here we show that Huisman & Millar misunderstood several important points in our article, and we explain why their criticisms do not challenge our original conclusions.

INTERPRETATION OF HERBARIUM RECORDS

Huisman & Millar (2013) contend that using herbarium records to assess historical change is ‘flawed’ because collections are unsystematic in space and time, and these data provide information on only presences, not absences. They aptly state that the presence of a species at a particular site in an early collection period followed by its absence at that site in a later collection period does not prove that the species has become locally extinct. However, this observation does not challenge our analysis or results because our inferences were not based on site- or species-specific

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extirpations. Huisman & Millar inherently assume that particular species and locations are of ‘fixed’ interest (*sensu* Shaffer *et al.* 1998). This is perhaps not surprising given their emphasis on phycological taxonomy but they do not appear to acknowledge the validity of different approaches. We did not analyse the presence or absence of species at sites, nor did we mention or discuss extirpations of particular species from specific sites. We analysed the geographical position of records as representing species distributions, and our interpretations concerned shifts in temperate floras based on a comparison of the median ‘before-and-after’ position of extreme records of ‘random species’ from ‘random locations’ (‘random’ is used *sensu* Shaffer *et al.* 1998). This approach is not predicated on a need to resample the same sites in both time periods (Shaffer *et al.* 1998). Our approach, like that of the many examples listed below, does assume that herbarium records contain useful and interpretable information about species’ distributions in space and time.

Huisman & Millar (2013) argue that our assumption that collections reflect species distributions is ‘questionable at the best of times, but becomes untenable when records are divided over time periods’. Nevertheless, herbarium records and other presence-only natural history collection data are often used to describe species’ distributions in space and time (e.g. Stadler *et al.* 1998; Delisle *et al.* 2003; Hickling *et al.* 2006; Fuentes *et al.* 2008; Saintilan 2009; Zuckerman *et al.* 2009; Rivers *et al.* 2011; Feeley 2012). Rivers *et al.* (2011) tested how many herbarium records were required for reliable range estimates for use in conservation assessments. They found that five herbarium records were sufficient to describe accurately the range-based conservation rating of 70% of hundreds of species of legumes and orchids in Madagascar (with 10 records, accuracy increased to 90% of species). Rivers *et al.* (2011) also found that ‘old’ and ‘new’ herbarium records reproduced range-based conservation estimates equally well. Also in Madagascar, Pearson *et al.* (2007) assessed the ability to predict the environmental niche of geckos from scarce occurrence data and found a high success rate with as few as five records. These studies support the idea that historical comparisons are possible even from relatively few records.

Considerable thought has gone into understanding the conceptual issues of using herbarium and other natural history collection (presence-only) data to detect changes in distribution (reviewed in Shaffer *et al.* 1998; Tingley & Beissinger 2009). Comparison of presence–absence vs presence-only data has shown that analyses based on presence-only data are not inherently flawed (Brotons *et al.* 2004). The lack of absence information does not affect our range analysis because it was not based on identifying species- or location-specific extirpations (absences), nor was it based on distribution models that generally predict ranges more accurately when absences are included (Brotons *et al.* 2004). For our community analysis, the lack of information on absences does not prevent useful interpretations of the multivariate patterns. Indeed, multivariate ‘presence–absence’ analyses based on presence-only data have provided useful insights into the ecology and biogeography of algae and higher plants in many instances (e.g. Peat *et al.* 2007; Phillips & Huisman 2009; Saintilan 2009; Waters *et al.* 2010). In conclusion, it is well established that herbarium and

presence-only data can provide useful information to detect spatiotemporal changes to species distributions.

GROUND-TRUTHING

Huisman & Millar (2013) criticise the lack of field validation of purported extirpations. As we have stated, our study did not identify local extinctions of *specific species* from *specific sites*, but it identified a shift in the median position of extreme records from assemblages of temperate species (Wernberg *et al.* 2011). Within this analytical framework, each individual range shift represents a random sample from a temperate flora. The accuracy of each of these random samples is associated with an unknown error, but collectively they will be distributed around the mean for the flora on average following the central limit theorem. Importantly, this implies that identifying unique errors in any of these range shifts would not invalidate our analysis of the means (or medians) and, therefore, that ground-truthing is not necessary to support our conclusion. Moreover, field validation of the nature suggested by Huisman & Millar theoretically requires observations that rule out each and every possible occurrence. Logically, this is not possible, and advocating ‘ground-truthing’ as a prerequisite to establish extinction runs counter to the entire disciplines of palaeontology, extinction biology and biogeography because few extinctions are ever observed directly given the minuscule probability of sampling individuals from declining populations at low densities (Bradshaw *et al.* 2012).

Other related studies that also illustrate the usefulness of natural history collections for historical analyses have not been undermined by the difficulty of acquiring field validations. For example, Delisle *et al.* (2003) used herbarium records alone to determine changes in distribution of six invasive wetlands species in Canada during the 20th Century. Similarly, Last *et al.* (2011) used a range of anecdotal and collections data to document poleward shifts in fish distributions over the past 100 years in eastern Australia, and Case *et al.* (2007) used herbarium records to document 150 years of nationwide declines in abundance of American ginseng (*Panax quinquefolius* Linnaeus) in the United States. In some circumstances, we do see the value in attempts to identify whether specific species have gone locally extinct or changed their distributions. For example, intensive surveys for one species listed in our appendix, the furoid *Scytothalia dorycarpa* (Turner) Greville, has revealed recent extirpation and a 100-km range contraction in Western Australia (Smale & Wernberg 2013), which is consistent with the trends reported in our original article (Wernberg *et al.* 2011). In conclusion, ground-truthing is not a necessity for the interpretation of changes to species distributions from natural history collection data.

COLLECTION EFFORT

One of the key criticisms from Huisman & Millar (2013) relates to ‘an incorrect interpretation of collection effort’. Collection effort is important because it is proportional to

the likelihood of sampling a target species if it is present and because several studies have demonstrated how uneven collection effort in space and/or time can bias estimates of changes in distribution in the direction of oversampling (Skelly *et al.* 2003; Shoo *et al.* 2006; Hassall & Thompson 2010; Feeley 2012). In other words, the likelihood of detection will be greatest where there are more collections.

Huisman & Millar (2013) suggest that the most meaningful gauge of collection effort would refer to the sites of historical range limits. We recognize that this can be important if the analyses aim to identify species-specific local extirpations (e.g. Phillips & Blackshaw 2011), but it makes less sense in our analysis in which we focused on flora-wide shifts in distribution across a broad geographic gradient. Specifically, focusing only on specimens collected around the site of the previously known range limit would not help identify a shift *per se*, and it would introduce the problem of ‘assumed absences for nondetection’ (Shaffer *et al.* 1998). Neither would it take into account that some species could move in the opposite direction (e.g. if geographical limits are not influenced mainly by climate), which turns out to be a common observation (Hickling *et al.* 2006; Lima *et al.* 2007; Zuckenberg *et al.* 2009; Sorte *et al.* 2010). We argue that in a study like ours, effort should encompass the entire area of interest, including sites outside the species’ current distribution where they could conceivably be found.

We identified differences in collection effort (volume) north and south of the tropical–temperate transition (31°S), and we identified differences between the early and late sampling periods for both coastlines (fig. 1A in Wernberg *et al.* 2011). Huisman & Millar (2013) show (their fig. 1) that on the west coast, much of the northern effort in the late period (1990–2009) was located north of 25°S. We included these records in our original analysis because they fell within our defined limits for the west coast and because we did not want to exclude (and therefore bias) the possibility of northward shifts for temperate species originally restricted to 25–27°S. Importantly, the northward collection bias persists even if we exclude specimens collected north of 25°S, with more than double the effort in the late compared to the early period (Fig. 1). The bias depends on the difference in northern collection effort between early and late collection periods (Shoo *et al.* 2006) and not the difference between northern and southern effort within each period as Huisman & Millar erroneously have argued. That is, by increasing the collection effort in the northern region in the later period (relative to the early period), the likelihood of resampling a species if it is in the northern region is increased. Therefore, this bias in collection effort is more likely to cause an apparent *northward* shift, which contrasts with the net *poleward* shift we detected. It also means that it is incorrect when Huisman & Millar claim that our figure (fig. 1A in Wernberg *et al.* 2011) does not support a northward collection bias on the east coast. Finally, the collection effort reported by Huisman & Millar (2013; fig. 1) does not contradict the patterns we reported, in part because they report only collection effort from the later collection period and in part because their 30–33°S latitudinal band encompasses effort both north and south of 31°S.

Collection effort can be defined as the total number of specimens collected (collection volume; e.g. Delisle *et al.* 2003; Fuentes *et al.* 2008), although the number of collection events (collection frequency) might also be a useful measure of effort. For our west coast data set, patterns of collection volume and frequency (Fig. 1) were similar ($r = 0.93$, $P < 0.0001$, $n = 12$), and for both measures there was a strong positive correlation between effort and collection of target species ($r = 0.93$, $P < 0.001$, and $r = 0.72$, $P = 0.042$, $n = 8$, for collection volume and frequency south of 25°S, respectively). This correlation supports the idea that total collection volume is a reasonable proxy for effort (probability of sampling) relating to temperate species.

Huisman & Millar (2013) also note that many records from the west coast in the later collection period (1990–2009) were from the Houtman Abrolhos Islands (~ 50 km off the mainland around 28–29°S) and so should be discounted because many species at the islands have tropical affinities. However, Huisman (1997) previously reported that ‘the algal flora of the islands includes a mixture of typically temperate species along with many species usually found at more northern latitudes’. Moreover, based on the absence of herbarium specimens of tropical species from the mainland, Phillips & Huisman (2009) found that the islands were characterised by the unusual presence of tropical species, not the absence of temperate species, and they concluded that ‘some temperate species, at least, are found at comparable latitudes to the Houtman Abrolhos Islands on the mainland’. We therefore argue that it would be unreasonable to discount these records as part of the overall collection effort because these records represent collection effort from sites where temperate species are commonly found. In conclusion, both our original (Wernberg *et al.* 2011) and our additional analysis of collection effort (Fig. 1) demonstrate conservative interpretations of changes to species ranges.

CRITERIA FOR DATA INCLUSION

Huisman & Millar (2013) also argued that our focus on temperate species is an ‘idiosyncrasy’ that causes an apparent southward shift in our analysis. Our range analysis focused on temperate species with a distribution limit north of 31°S (tropical–temperate transition zone) in the early period (1940–1959) because the inclusion of widespread species – and species where poleward shifts would be constrained by the east–west orientation of the south coast – would not be informative (Hassall & Thompson 2010). Many studies have limited range analyses to taxa in which change can be expected because of their affinity and distribution limits within a study region (e.g. Hickling *et al.* 2006; Feeley 2012). On the basis of Huisman & Millar’s argument, a negative relationship between the northernmost latitude of collection in the early period (1940–1959) and the recorded range shift would be expected (i.e. the closer the record to the ‘true’ northern range limit, the greater the expected shift). Yet we found no evidence for such a relationship. The northernmost latitude of collection in the early period explains less than 2% of the observed range shift ($r^2 = 0.018$, $P = 0.374$, $n = 45$). In addition, the purported ‘idiosyncrasy’ is inconsistent with

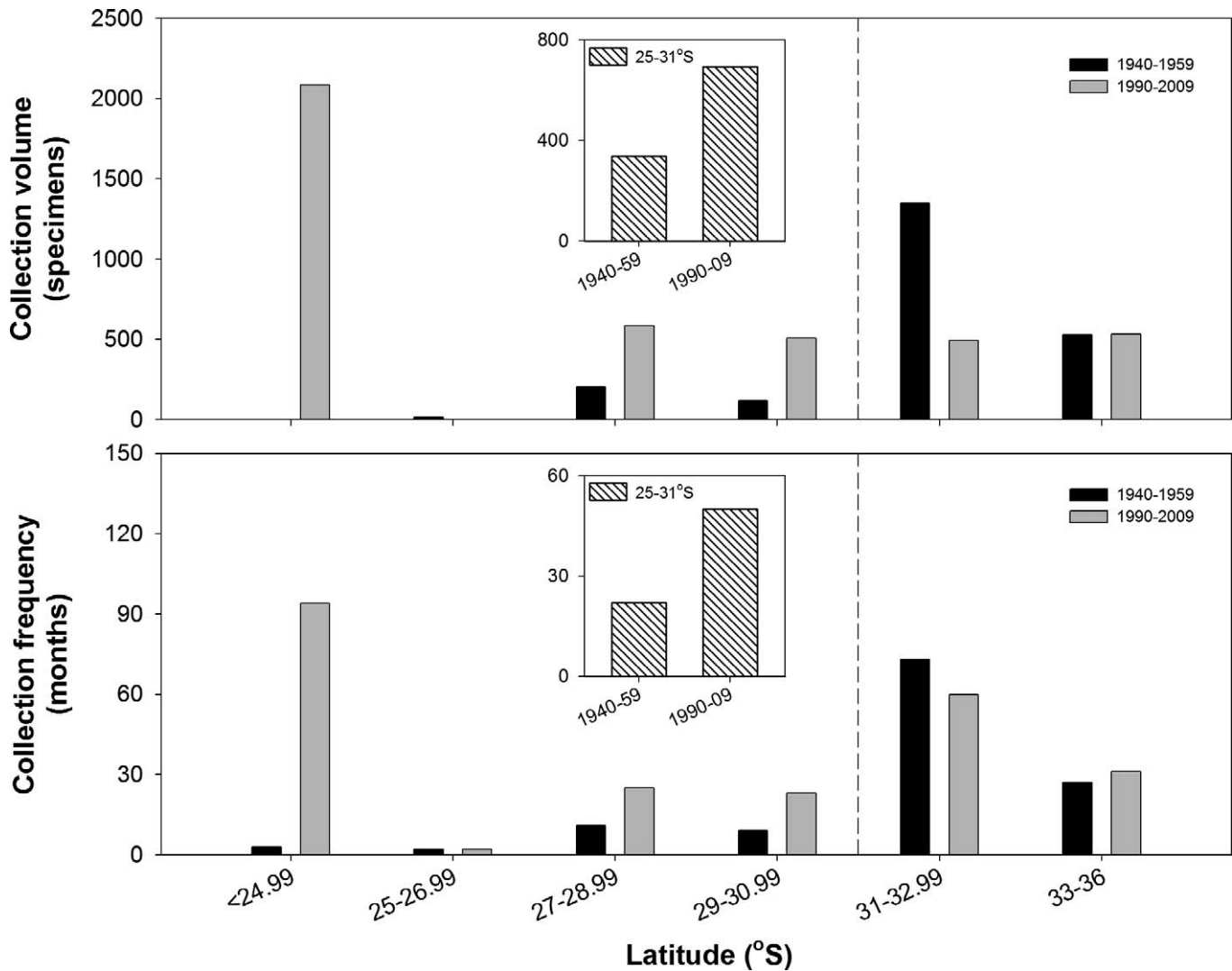


Fig. 1. Collection effort of seaweed herbarium records from the west coast of Australia measured as collection volume (top: the number of specimens lodged and collection frequency (bottom: the number of unique months that specimens were collected). The vertical dashed line indicate 31°S , the tropical–temperate transition zone used in Wernberg *et al.* (2011) to divide northern and southern records. The inserted panels show the summed collection effort between 25 and 31°S in the early and late periods, respectively. Between 25 and 31°S , the grey bars are larger than the black bars, indicating higher sampling effort in the later period, also indicated by the insert where values have been added.

the findings that 15% and 44% of the species on the east and west coasts, respectively, shifted northward (Wernberg *et al.* 2011). It is possible that restricting species to those recorded north of the tropical–temperate transition zone in the early period could create an apparent southwards shift – not because the species are temperate *per se* but because it restricts the analyses to species with a more accurate estimation of the ‘true’ limit in the early period; whereas, it does not impose the same restriction on species from the later period. However, our additional criterion for at least five records in the later period counters a potential southward bias and instead created a northward bias because it increases the likelihood of capturing the ‘true’ range limit in the late period (Shoo *et al.* 2006). This is reflected in the rapidly decreasing probability of generating the observed range shift by chance with increasing recording requirements in the late period (N2, Fig. 2). That is, in contrast to the observed poleward shift in range limits, a net

northward shift would be anticipated in the absence of any climatic forcing or changes to distribution patterns.

Finally, Huisman & Millar state that we did not validate our decision to focus on species with ≥ 5 records in the late period, but in the electronic appendix to our article, we presented additional analyses, repeating the calculations for six different subsets of species, imposing selection criteria of ≥ 5 and ≥ 10 records in the later period, within 10-, 20-, and 30-year time segments and for both the east and the west coast data sets (Wernberg *et al.* 2011). These sensitivity analyses demonstrated that our results were robust to the choices of records and time segments on two independent coastlines; compared to the median shifts of -0.46°S and -1.92°S reported in our article, the median shifts across these sensitivity tests were $-0.38^{\circ}\text{S} \pm 0.09$ SE ($n = 6$) and $-1.89^{\circ}\text{S} \pm 0.27$ SE ($n = 5$) on the west and east coasts, respectively (Wernberg *et al.* 2011).

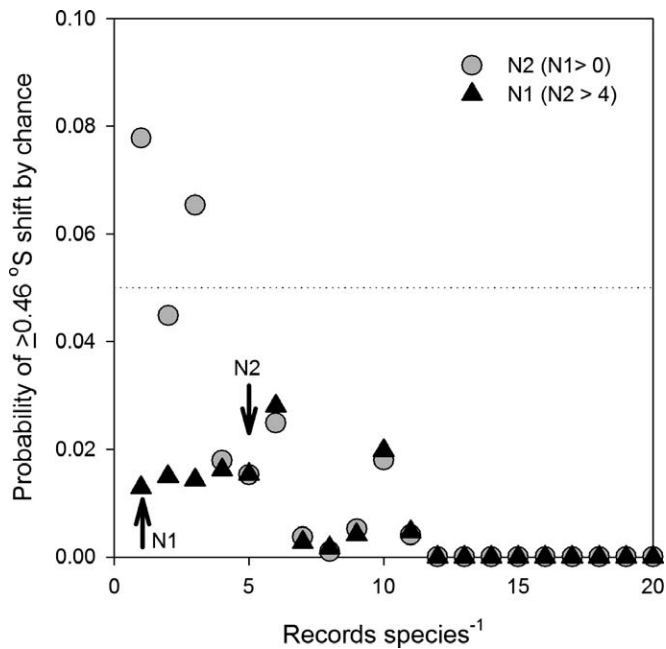


Fig. 2. Likelihood of generating a poleward shift of $\geq 0.46^\circ$ latitude by chance alone at different collection frequencies (number of records) in the early (N1, 1940–1959) and the late (N2, 1990–2009) periods. Arrows indicate species inclusion criteria applied in Wernberg *et al.* (2011). Probabilities generated by 10,000 repeated calculations of range shift for each N1 or N2. For each calculation, records were randomly assigned (without replacement) to species from the pool of records of temperate species with a maximum latitude of record north of 31°S in the early period. The number of records in the early period (N1) has relatively little influence (because we focused only on temperate species north of 31°S). Also, the probability of generating the observed range shift drops rapidly with an increasing number of records in N2, and the probabilities of generating such a pattern at random were low given the criteria we employed.

To test the probability of generating a poleward shift of $\geq 0.46^\circ$ latitude by chance alone, at different collection frequencies (number of records) in the early (N1, 1940–1959) and the late (N2, 1990–2009) periods, we constructed a series of randomization tests for different values of N1 and N2 (Wernberg *et al.* 2011). We generated probabilities by 10,000 repeated calculations of range shift for each N1 or N2. For each calculation, we randomly assigned records (without replacement) to species from the pool of records of temperate species with a northernmost latitude of record north of 31°S in the early period. These tests show that given the selection criteria we employed, there was a small ($P < 0.05$) probability that the observed median poleward range shift could have happened by chance (Fig. 2). Therefore, our criteria for data inclusion were based on established concepts, and they were supported by sensitivity analyses.

CONCLUSION

We used herbarium records to test the hypothesis that temperate seaweed floras in Australia have shifted latitudinally over the past five decades of documented warming. We provided multiple lines of evidence (community, range,

and sensitivity analyses from two independent coastlines) to demonstrate a net poleward shift. Huisman & Millar do not contest that temperate seaweeds might have retreated poleward (Brodie *et al.* 2009; Millar 2009; Huisman & Millar 2013), but they criticised our methods and argued that the assumption that herbarium data can reflect species distribution in space is ‘questionable at the best of times’ and over time become ‘untenable’ and need field verification (Huisman & Millar 2013). We reply by showing that we have carefully and comprehensively considered the issues of using herbarium and other natural history collection (presence-only) data to detect changes in distribution (reviewed in Shaffer *et al.* 1998; Tingley & Beissinger 2009). Our analysis of presence-only data uses the approach of comparing extreme records of random species from random locations (*sensu* Shaffer *et al.* 1998) rather than focusing on particular candidate species and their subsequent loss from specific sites. Hence, the need for ground-truthing of extinctions is of limited value to the interpretation of our analysis. Herbarium records and other natural history collections contain valuable historical information. The limitations of these data sources should not – and clearly have not – prevented a growing use of natural history collections as valuable baselines for detecting biological responses to climate change (reviewed in Shaffer *et al.* 1998; Tingley & Beissinger 2009).

Originally, herbaria and their collections were not intended for such purposes. However, if we cannot find ways to broaden the use of the data we collect and, in turn, encourage novel scientific approaches, then our discipline will not be able to evolve to explore difficult questions.

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