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Time, mediated through plant versatility, is a better predictor of medicinal status of alien plants

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Abstract: Ethnobotany has been, for too long, a descriptive discipline. However, ethnobotanists are increasingly calling for a paradigm shift towards the formulation of unifying theories and hypothesis-driven research in ethnobotany. Here, we formulated a theory, termed *time-since-introduction theory*, to explain the integration of alien plants into local pharmacopoeias in their recipient environment. This theory suggests that the factor *time* is paramount in determining which alien plants are more likely to be included in the medicinal flora of the areas they are introduced in. The theory relies on three hypotheses, the *availability* and *versatility* hypotheses alongside the *residence time hypothesis* newly proposed in the present study. We tested this theory by fitting a structural equation model to ethnobotanical data collected on South Africa's alien woody flora. Although residence time is a direct predictor of medicinal status of alien plants, it is a better predictor when mediated through plant versatility. These findings are in support of the theory, and we consequently proposed a framework with which to understand different paths linking all three hypotheses. Collectively, our study shows the value of time in the development of ethnobotanical knowledge and fully responds to the pressing call for paradigm shift in ethnobotany.

Keywords: Alien plant species, Availability hypothesis, Versatility hypothesis, Residence time hypothesis, theory driven ethnobotany

1. Introduction

Most ethnobotanical studies are more interested in documenting people's knowledge of useful plants to humans and what these plants are used for [1,2]. Recently, an increasing number of authors are calling for the vast wealth of ethnobotanical knowledge documented over centuries to be used to test hypotheses and theories or to formulate new ones [3-13], a common practice in any scientific discipline. Some authors even questioned whether ethnobotany, as a scientific discipline, has a unifying theory, since the discipline remains, for too long, largely descriptive without clearly defined theoretical frameworks [13-16]. Consequently, there has been repeated calls for a para-

digim shift towards more theory-inspired or hypothesis-driven research in ethnobotany [12].

While a hypothesis is a preliminary proposed explanation for an observation, a theory is an “integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of a scientific observation” [17]. Here, we proposed a theory, termed *time-since-introduction theory* to explain the integration of alien plants into local medicinal flora. This theory integrates three hypotheses, two of which are already known in ethnobotany – the availability [18,19] and *versatility* hypotheses [20,21] – and a third hypothesis newly defined in the present study, that is, the *residence time hypothesis*.

The *availability hypothesis* suggests that easily accessible or locally abundant alien plants are more likely to be used for medicine in their invaded regions [18,19], and evidence for this has also been showed even for native species (e.g., [7,22]). The *versatility hypothesis* predicts that alien plants that have multiple non-medicinal uses for humans (food, ornamental, etc.) are more likely to be eventually used for medicine in their invaded regions [20,21]. Although these two hypotheses were supported in many studies [12,22], they did not account explicitly for the factor *time* in the development of medicinal knowledge for alien species, although the development of medicinal knowledge is time-dependent, i.e., it follows a dynamic process over time (e.g., [23]) shaped by the environment [5]. Consequently, we propose a new hypothesis – termed the *residence time hypothesis* – that explicitly highlights the factor *time* in the development of ethnobotanical knowledge. We formulate this hypothesis as follows: the *residence time hypothesis* predicts that the longer the residence time of an alien plant in a new environment, the more likely it is for the plant to be integrated into local medicinal flora. Although ref. [23] did not explicitly define the *residence time hypothesis*, their study already evoked the value of the factor *time* in the development of traditional medicinal knowledge: the longer people are surrounded by certain plants, the more time for trial, error, and communication with other people, the more likely they use the plant as medicine, and the more likely the medicine is effective.

The aim of the present study is to propose a theoretical framework that integrates several hypotheses to shed light on how medicinal knowledge is developed on alien plants in their invaded environment. Alien plants are one of the major threats driving the ongoing biodiversity crisis [24], and global efforts are devoted to fight these threats, particularly in South Africa where tremendous financial resources have been spent on alien species control but unfortunately with mixed successes [25]. However, since humans, in general, select and move these alien species around, there is a social dimension to biodiversity conservation [26], including the dynamic of alien species populations and control that cannot be ignored if we are to be successful. It is impossible for socially driven environmental problems to be solved effectively if provided solutions are not understood, adopted, and implemented by and with local people [27]. The question now is: how could ethnobotanical knowledge be valuable in conservation science [28] if we have poor or limited understanding of the mechanisms driving plant selection and use by local people? These mechanisms behind plant selection and use can be understood only if ethnobotanists use the wealth of descriptive plant use data documented over centuries to conduct hypothesis- and theory-driven studies [12,13,16].

In the present study, we aim to demonstrate how the three hypotheses (*availability*, *versatility*, and *residence time* hypotheses) could be integrated into a single theoretical framework termed *time-since-introduction theory* to explain the integration of alien plants, outside their native ranges, into local pharmacopoeias. To illustrate our theoretical framework, we used the alien woody flora of South Africa, a country well-known for the incredible richness of its native flora (24,000 vascular plants, and three biodiversity hotspots [29]) as a model. A complete list of alien woody plants as well as their years of introduction into South Africa was compiled (Table S1), allowing us to determine their residence time from the year of introduction of the plant species into South Africa to the year 2018 where the statistical analysis reported in the present study was done. In addi-

tion, several variables pertaining to ethnobotanical knowledge were also collected (Table S1): total uses recorded for each alien plant (medicinal and non-medicinal uses), its medicinal status (a binary variable defined as non-medicinal versus medicinal), number of recipes reported for the alien plants, number of plant organs used medicinally and the availability of the alien plant.

2. Materials and Methods

2.1. Study area.

The test of *time-since-introduction* theory was based on South Africa's alien flora. South Africa is well-known for its megadiverse flora as well as its diverse cultural groups with incredible wealth of medicinal knowledge [29].

2.2. Data Collection

2.2.1. *The South Africa's alien woody flora and residence time*

Our dataset of alien woody plants and their years of introduction to South Africa were obtained from a previously published study by ref. [30]. The dataset represents the most comprehensive checklist of alien woody species, combining datasets of refs [31,32] and ref. [33] with local experts' knowledge from all major research institutions and academic centres working on alien plants in South Africa [30]. In total, our dataset represents 210 alien woody plants (Table S1) used for various hypothesis-testings in our research group (e.g., [22,34]).

2.2.2. *Availability, Versatility, and medicinal use data of alien woody plants*

The occurrence of each alien species was documented using various resources, but mainly the Global Biodiversity Information Facility [35] and regional and online local flora databases and ethnobotanical publications [36]; Flora of Botswana, <http://www.botswanaflora.com/> accessed; Flora of Mozambique, <http://www.mozambiqueflora.com>, accessed 2017; Flora of Southern Africa, <http://posa.sanbi.org.www57.cpt1.host-h.net/flora/browse.php?src=FloraSA> accessed 2018; Flora of Zimbabwe, <http://www.zimbabweflora.co.zw/>, accessed 2017; Trees Atlas of Namibia, <http://treeatlas.biodiversity.org.na/> accessed 2017; Prelude Database for Medicinal Plants in Africa, http://www.africamuseum.be/en/research/collections_libraries/biology/prelude, accessed 2017). This information is available in Table S1.

We documented through an intensive literature search the different services these species provide to humans in southern Africa. First, we used the Web of Science (WoS) to retrieve existing scientific ethnobotanical studies in the region. Second, we performed search for each species by using combinations of keywords such as "scientific name of species", "South Africa", "uses", "usages", "Utilisation" and "benefit". We also made use of Google and Google Scholar for scientific and grey literature using similar keywords to retrieve online resources such as regional and country-specific journals, proceedings, technical reports, herbarium and commercial websites informing on the uses of woody plants in our dataset. The Southern African Plant Invaders Atlas (<http://www.agis.agric.za/wip/>, accessed on March 1st, 2017) was also consulted. In addition, we consulted key books on the regional flora such as *Trees of Southern Africa*, *Field Guide to Trees of Southern Africa*, and *Guide to Trees Introduced into Southern Africa* [33,36,37]. Additionally, the *Prelude Database for Medicinal Plants in Africa* (<http://www.africamuseum.be/collections/external/prelude>; accessed on 10 February 2017) was also consulted. All the different uses retrieved from this wide and intensive literature search were grouped into 12 distinct categories of services ranging from medicinal use to ornamental and spiritual use (Table S1). From all these sources, further information of the number of recipes and organs used to treat specific ailments were retrieved. Documented information on the number of recipes and organs used by identified

medicinal alien woody plants is found in Table S1. Number of organs are total numbers of organs or parts of the plant used medicinally. For analysis purpose, the medicinal status was coded as 0 (non-medicinal) and 1 (medicinal).

2.3. Data analysis

The relationships between all variables were tested by fitting a structural equation model (SEM) using the function *psem* implemented in the R package piecewise-SEM [38]. An SEM is a multivariate and powerful technique used to test and evaluate a theoretical framework, that is, a multivariate causal relationship [39]. The benefit of an SEM is that various causal relationships can be defined and tested simultaneously.

Five statistical models were included in the SEM, and each of them was grounded on the following rationale. First, the variable *availability* was modelled as a function of residence time, assuming that early introduced alien species (longer residence time) would be more available to local people than recently introduced alien. Second, the variable *number of recipes* was modelled as a function of medicinal status (i.e., for a species to have a medicinal recipe, it has to be first and foremost medicinal), availability (i.e., available species are more likely to be used for medicine as predicted by availability hypothesis), residence time (i.e., the longer the residence time of an alien plant, the more medicinal recipes will be developed for that species by local people). Third, we modelled '*medicinal status*' as function of residence time (residence time hypothesis), availability (availability hypothesis) and total uses (i.e., versatility hypothesis). Fourth, the variable '*total uses*' was modelled as a function of residence time and availability, assuming that the longer the residence time, the more available the alien species and the more uses (e.g., medicinal, food, horticultural uses, etc.) will be established by the local people. Finally, the fifth model included in the SEM was developed for the variable '*number organs used*' as a function of medicinal status, the number of recipes, residence time and total uses. This fifth model is based on the assumption that the use of several different organs medicinally means i) the plant is medicinal (medicinal status), ii) it has more recipes that involve several organs (number of recipes), iii) the plant has been around for longer enough time (residence time) so that multiple uses have been established for it in the local community (total uses).

The adequacy of the SEM fitted was assessed using its overall Goodness-of-fit (C value) and the p value. The parameter C is indicative of whether the SEM is good enough to explain the data such that the lower the C value the better the SEM for the data. The p-value here is interpreted as follows: $p < 0.05$ means the SEM departs significantly from the best fit and therefore should be rejected; $p > 0.05$, on contrary, means the SEM is not different from the best fit and therefore can be used to explain the data [38,40].

Each of these five models that form the SEM was fitted using the R function *glmer.nb* (negative binomial generalised linear mixed effect models), except for the model of '*medicinal status*' for which the R function *glmer* was instead used. For four of the response variables that are 'count data' (availability, number of recipes, total uses and number of organs used), the negative binomial distribution was used to account for over-dispersion [41], and the binomial error family was used for '*medicinal status*' since it is a binary variable (medicinal versus non-medicinal). Also, the shared evolutionary history among South Africa's alien species [34] justified our used of mixed effect model (GLMER). The R script used for this analysis is provided in the Supplemental Information.

3. Results and Discussion

Our analysis shows that the fitted SEM is an appropriate meta-model (theoretical framework) that explains how medicinal knowledge could relate to residence time and other ethnobotanical variables such as plant availability and versatility (Fig. 1; Fisher C = 0.54; df = 4, P = 0.96).

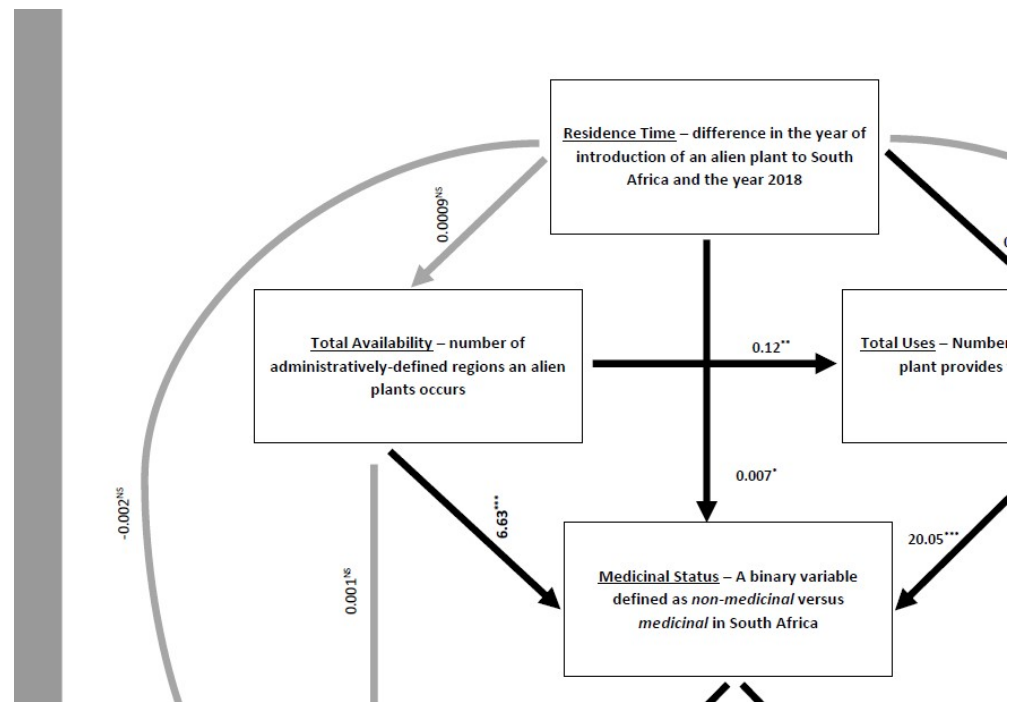


Figure 1. Theoretical framework (Structural Equation Model) proposed and tested in this study to explain the *time-since-introduction* theory. Thick black arrows indicate significant relationships while grey arrows are non-significant relationships. Numbers on arrows are path coefficients. * Indicates level of significance of a relationship at $\alpha=0.05$; When a relationship is not significant but close to significance level, its value is rather mentioned instead of stars (*). ns = non-significant.

Specifically, our SEM reveals different paths through which residence time predicts medicinal status of alien plants (Table 1). Firstly, there is a direct path with a positive significant relationship such that early introduced alien plants tend to be medicinal than not (Fig. 2a; $\beta_1 = 0.007 \pm 0.002$, $P=0.014$), supporting the *residence time hypothesis*. Secondly, residence time also predicts medicinal status, but this relationship is mediated through plant availability [residence time \rightarrow availability ($\beta_{2.1} = 0.0009 \pm 0.001$) \rightarrow medicinal status ($\beta_{2.2} = 6.6288 \pm 0.002$)] such that the coefficient for this indirect path is $\beta_2 = \beta_{1.2} \times \beta_{2.2} = 0.005965$. This availability-mediated relationship between residence time and medicinal status is in support of the availability hypothesis which predicts that alien species that are more accessible to people or more abundant stand a better chance of being integrated into local medicinal flora than species that are rare or are of restricted distribution range [18,19]. This hypothesis has been employed to explain medicinal uses of, not only native plants [7] but also the incorporation of alien plants into local pharmacopoeias [8,42]. The metrics of availability of a given plant have been variously defined, including the distance from people's home to the location of the plants in the wild or the price of the plant in the traditional medicinal market [43]. Recently, the presence/absence of a plant in administratively delimited regions has also been used to define its availability [8]. This recent definition of availability was used in the present study.

Table 1. Coefficients of all relationships tested in the Structural Equation Model (SEM) that illustrates the *time-since-introduction* theory. P values in bold correspond to statistically significant relationships. Two of the relationships were only marginally significant ($P < 0.10$) but the remaining significant relationships were so at $P < 0.05$.

Responses	Predictors	Estimate	Std. Error	DF	Crit. Value	P. Value
Availability	Residence time	0.0009	0.0010	108	0.8538	0.3932
Number of medicinal recipes	Availability	0.0018	0.1002	101	0.0181	0.9856
Number of medicinal recipes	Residence time	-0.0012	0.0024	101	-0.4986	0.6181
Number of medicinal recipes	Medicinal status	23.1849	2.0860	101	11.1144	0.0000
Medicinal status	Residence time	0.0068	0.0028	108	2.4456	0.0145
Medicinal status	Availability	6.6288	0.0020	108	3383.6146	0.0000
Medicinal status	Total uses	20.0485	0.0014	108	14009.9666	0.0000
Total uses	Residence time	0.0016	0.0009	108	1.6691	0.0951
Total uses	Availability	0.1155	0.0392	108	2.9500	0.0032
Number of organs used medicinally	Number of medicinal recipes	0.0734	0.0404	101	1.8162	0.0693
Number of organs used medicinally	Medicinal status	23.6634	2.9541	101	8.0103	0.0000
Number of organs used medicinally	Residence time	0.0009	0.0024	101	0.3566	0.7214

Number of organs used medicinally	Total uses	0.1134	0.1234	101	0.9187	0.3582
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Thirdly, residence time also predicts indirectly medicinal status, but this relationship is mediated by total uses [residence time \rightarrow total uses ($\beta_{3.1} = 0.0016 \pm 0.0009$) \rightarrow medicinal status (Fig. 2b; $\beta_{3.2} = 20.0485 \pm 0.0014$)] such that the coefficient for this indirect path is $\beta_3 = \beta_{3.1} \times \beta_{3.2} = 0.032$. This relationship mediated by total number of uses matches the prediction of versatility hypothesis which suggests that alien plants that have multiple uses are more likely to be integrated into local medicinal flora in their new environment [20-22]: alien plants can first be introduced into a new geographic region primarily for diverse services including food, construction materials, ornamental, etc. and then be used at a later stage for medicinal purpose when the need to fill some therapeutic gaps in local pharmacopoeias arises [8,20,46].

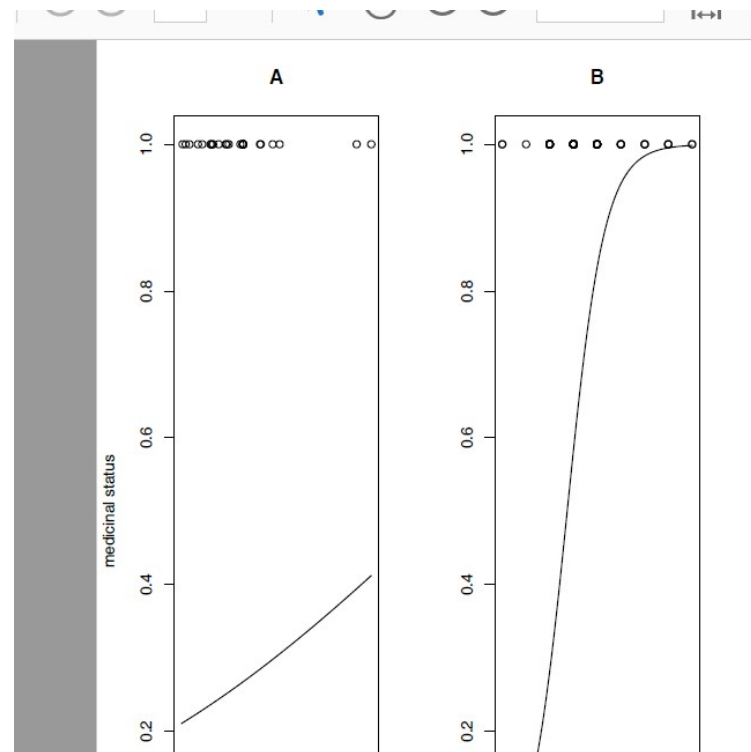


Figure 2. Significant relationships in the theoretical framework defining the *time-since-introduction* theory. Relationships between medicinal status and residence time (a), total use (b) and availability (c).

The last path linking residence time to medicinal status is mediated through both availability (Fig. 2c) and total uses [residence time \rightarrow availability ($\beta_{4.1} = 0.0009 \pm 0.001$; Fig. 3a) \rightarrow total uses ($\beta_{4.2} = 0.1155 \pm 0.0392$; Fig. 3b) \rightarrow medicinal status ($\beta_{4.3} = 20.0485 \pm 0.0014$)], but this path shows the lowest coefficient $\beta_4 = \beta_{4.1} \times \beta_{4.2} \times \beta_{4.3} = 0.00208$. It is therefore clear that the path with the highest coefficient is the indirect path mediated through total uses ($\beta_3 > \beta_1 > \beta_2 > \beta_4$), suggesting that not only residence time directly predicts the medicinal status of alien plants but that the most important predictive power of residence time is mediated by plant versatility (see ref. [22]).

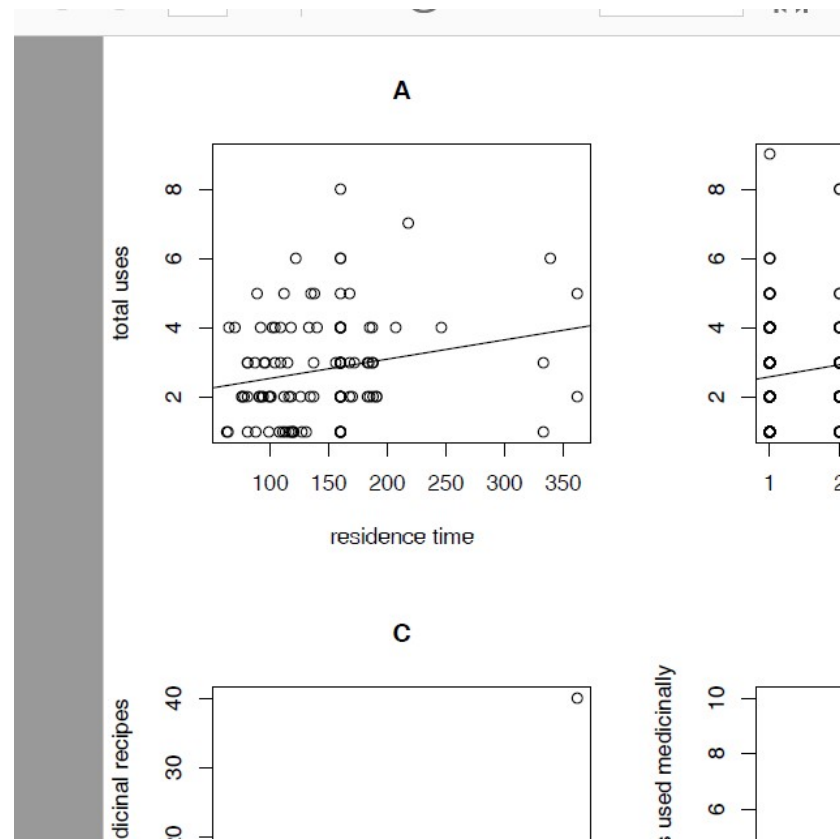


Figure 3. Additional significant relationships in the theoretical framework defining the *time-since-introduction* theory. Relationship between total uses and residence time (a), total uses and availability (b) and between number of recipes and medicinal status (c) as well as between number of organs used medicinally and medicinal status (d).

In addition, our SEM analysis indicates that medicinal status correlates with both number of recipes (i.e., medicinal plants are more likely to have some recipes than not, $\beta = 23.18 \pm 2.08$, $P < 0.001$, Fig. 3c) and number of organs medicinally useful ($\beta = 23.66 \pm 2.95$, $P < 0.001$, Fig. 3d) while medicinal status itself is predicted by total number of uses (versatility hypothesis, $\beta = 20.04 \pm 0.001$, $P < 0.001$; [22]). Interestingly, early introduced alien plants to South Africa (longer residence time) tend to have higher number of uses than late-introduced species (shorter residence time), although the relationship is only marginally significant ($\beta = 0.0016 \pm 0.0009$, $P = 0.09$). These direct and indirect relationships provide clear evidence of how multiple hypotheses can be integrated to form a unifying theory in ethnobotany, a theory termed, in this study, as *time-since-introduction theory*.

In response to early calls to formulate testable theories in ethnobotany [15,45], several studies instead developed methodological rigor [46] and ethnobotanical indices [47]. In addition, other studies repeated the call for 'less quantification' and more theory-inspired and hypothesis-driven research in ethnobotany [12,48-50]. Current challenges and critics faced by ethnobotany define a critical period in the evolution of the discipline, a lengthy trajectory that other sister disciplines went through. In the 1990s, ecology, which is now well-known with several theories, was too questioned as the discipline had

then no general laws or a unifying theory [51-54]. Increasingly, ethnobotanists are taking the same trajectory, making use of the wonderful and unique descriptive ethnobotanical data documented for centuries across different geographic regions of the world to formulate and/or test various ethnobotanical hypotheses [3-11,16,55-57]. It has not been possible to test widely the residence time hypothesis of the introduction of alien plants into local medicinal flora simply because of the lack of data on the times of introduction of these species into their recipient environments. Fortunately, such historical data exist in South Africa and allow us to fill the knowledge gap in the present study. In the context of multiple calls for paradigm shift, the present study proposes and tests an ethnobotanical theory that integrates multiple hypotheses to explain the integration of alien plants into local medicinal flora. Here, the theory was tested on alien woody plants. We suggest that future studies test the theory on different life forms in different geographical contexts.

4. Conclusion

Ethnobotany is the discipline interested in the interactions of humans with plants. Most ethnobotanical studies have generated tremendous dataset on plant uses across the globe. However, calls to use existing dataset for more hypothesis and theory driven studies are now increasing. Here, we formulate, test, and provide evidence for the role the factor *time* plays in the process of including alien plants into local medicinal flora. We then provide a theoretical framework, termed *time-since-introduction hypothesis*, that integrates three ethnobotanical hypotheses in support of theory and call for more studies to test the theory with different datasets across different geographies.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: All variables collected and analyzed in this study; R script used to analyze the data in Table S1

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Conflicts of Interest: The authors declare no conflict of interest.

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